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EXPERIMENTS ON SEXUAL ISOLATION IN DROSOPHILA. III. GEOGRAPHIC STRAINS OF DROSOPHILA STURTEVANTI

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When females of different geographic strains of the same species are confined with males of one of these strains, the matings may occur either at random or preferentially, one kind of females being inseminated more frequently than the other. Relatively slight mating preferences have been observed in Brazilian and Guatemalan *Drosophila willistoni*,[1] and some quite striking preferences have been found in Brazilian, Guatemalan and Mexican strains of *D. prosaltans*.[2] Most of these intra-specific mating preferences are one-sided: greater proportions of females of one than of the other strain are inseminated by males of both strains. Data reported in the present article show, however, that two-sided preferences for homogamic matings, which are, in general, characteristic of interspecific crosses, occur also within the species *D. sturtevanti* Duda (= *D. biopaca* Sturtevant).

The strains of *Drosophila sturtevanti* came from Tamazunchale, state of San Luis Potosi, Mexico (obtained through the courtesy of Professor J. T. Patterson), Quiriguá, Guatemala (obtained through the courtesy of Professor A. H. Sturtevant), Belem, state of Pará, Rio de Janeiro, Federal District, and Bertioga, state of São Paulo, Brazil. The flies from all these strains are morphologically similar, intercross readily and give rise to fertile F_1 and F_2 progenies. The technique used in the experiments with *D. sturtevanti* is identical with that used for *D. prosaltans*,[2] except that *D. sturtevanti* females are dissected on the sixth or the seventh day after the making of the crosses. Sexual activity in this species starts late, in fact later than in other species of Drosophila with which the writer is familiar. Before the sixth day scarcely any females are inseminated, but on the eighth day only few remain not fertilized. The tubular (ventral) receptacle in *D. sturtevanti* is an extremely long tube, much longer than the body, resembling a skein of wool that is twisted, as a whole, into paired spirals lying on both sides of the vagina. Live spermatozoa can be seen in some, but usually not in all, coils. The large but transparent chitinous

spermathecae are, in inseminated females, only partly filled with a tangled mass of sperm.

The data are summarized in table 1. In every one of the 20 crosses a positive isolation index has been obtained, which suggests that males of all strains inseminate more of their own females than of those of other strains. The statistical significance of the observed deviations from random mating is measured by the χ^2's; values higher than 6.6 (corresponding to the 0.01 probability level) have been observed in 10 crosses, and values smaller than 2.7 (corresponding to the 0.10 probability level) in only 5 crosses. The highest isolation indices are found in the crosses of strains from the two geographically most remote localities (Tamazunchale in Mexico and Bertioga in Brazil), but localities nearly as remote (Tamazunchale and Rio de Janeiro) fail to show statistically significant isolation indices. Strains from geographically relatively close localities may either interbreed at random (Rio de Janeiro and Bertioga) or may display a considerable isolation (Tamazunchale and Quiriguá). Strains which show no isolation from each other (Rio de Janeiro and Bertioga) may behave very differently with respect to other strains (Tamazunchale, Belem, or Quiriguá).

TABLE 1

NUMBERS OF FEMALES DISSECTED (n) AND PER CENT CARRYING SPERM (%) IN VARIOUS CROSSES OF *Drosophila sturtevanti*

FEMALES	MALES	HOMOGAMIC n	HOMOGAMIC %	HETEROGAMIC n	HETEROGAMIC %	χ^2	ISOLATION INDEX
Tamazunchale, Quiriguá	Tamazunchale	194	60.3	192	37.0	21.0	0.24
Tamazunchale, Quiriguá	Quiriguá	104	46.2	107	24.3	11.1	0.31
Tamazunchale, Belem	Tamazunchale	111	54.1	109	32.1	10.7	0.25
Tamazunchale, Belem	Belem	86	65.1	82	41.5	9.5	0.22
Tamazunchale, Rio	Tamazunchale	104	52.9	112	46.4	0.9	0.06
Tamazunchale, Rio	Rio	124	61.3	130	49.2	3.7	0.11
Tamazunchale, Bertioga	Tamazunchale	115	73.9	104	35.6	32.6	0.35
Tamazunchale, Bertioga	Bertioga	108	58.3	108	24.1	26.2	0.42
Quiriguá, Belem	Quiriguá	106	48.1	97	25.8	10.9	0.30
Quiriguá, Belem	Belem	94	54.3	99	24.2	18.3	0.38
Quiriguá, Rio	Quiriguá	99	56.6	96	43.8	3.2	0.13
Quiriguá, Rio	Rio	116	50.0	113	35.4	5.0	0.17
Quiriguá, Bertioga	Quiriguá	99	49.5	103	32.0	6.4	0.21
Quiriguá, Bertioga	Bertioga	106	59.4	109	26.6	23.7	0.38
Belem, Rio	Belem	160	55.6	157	49.0	1.4	0.06
Belem, Rio	Rio	98	65.3	106	39.6	14.5	0.24
Belem, Bertioga	Belem	101	50.5	100	39.0	2.7	0.13
Belem, Bertioga	Bertioga	91	41.8	88	31.8	2.0	0.14
Rio, Bertioga	Rio	106	51.9	106	50.0	0.1	0.02
Rio, Bertioga	Bertioga	101	50.5	106	48.1	0.1	0.02

The situation found in *D. sturtevanti* is different from those in *D. willistoni*[1] and *D. prosaltans*.[2] In *D. sturtevanti* the rule seems to be that strains

from different regions show incipient sexual isolation—preference for homogamic matings and aversion from heterogamic ones. Random mating is the rule in *D. willistoni*, but both Guatemala and Brazilian males have in some crosses inseminated preferentially Brazilian females. In *D. prosaltans* there is a "hierarchy" of strains correlated with their geographic origin. Both northern and southern males inseminate preferentially northern females; therefore, in some crosses homogamic matings are more common than heterogamic ones (positive isolation indices), and in other crosses heterogamic matings are more frequent (negative isolation indices). The strains from Guatemala and Brazil show, however, a mutual aversion to interbreeding. *D. nebulosa* Sturtevant is another species in which preferences for homogamic as well as for heterogamic matings are observed. Strains of this species coming from state of San Luis Potosi, Mexico (kindly furnished by Professor J. T. Patterson), and from Belem do Pará, Brazil, have been used. The experiments on *D. nebulosa* were arranged exactly like those on *D. prosaltans* and *D. sturtevanti;* the dissections have been made on the fourth day after the crosses. A summary of the results is given in table 2. It is evident that when Brazilian and Mexican females are kept with Brazilian males, Brazilian females are inseminated preferentially; but when Mexican males are used there seems to be also an excess of inseminations of Brazilian females (a negative isolation index which is not quite significant statistically).

TABLE 2

NUMBERS OF FEMALES DISSECTED (*n*) AND PER CENT CARRYING SPERM (%) IN CROSSES OF *Drosophila nebulosa*

FEMALES	MALES	HOMOGAMIC *n*	HOMOGAMIC %	HETEROGAMIC *n*	HETEROGAMIC %	χ^2	ISOLATION INDEX
Mexican, Brazilian	Brazilian	126	78.6	133	41.4	37.1	0.31
Mexican, Brazilian	Mexican	113	42.5	113	55.8	4.0	−0.14

Two types of preferential mating have been observed in Drosophila. They are sexual isolation proper and one-sided mating preferences. Strains A and B are said to be sexually isolated if males of A mate chiefly with A, and males of B chiefly with B females (positive isolation indices). If the mating preference is one-sided, A males mate more frequently with A than with B females (positive isolation index), but B males show either no preference (isolation index close to zero) or a preference for A females (negative isolation index). Situations intermediate between true sexual isolation and one-sided mating preference occur. Theoretically, two strains may also show consistent preferences for heterogamic matings (negative isolation indices), but this has never been found in experiments.

Sexual isolation reduces the rate of gene exchange between the populations concerned; when the isolation is complete the gene exchange is altogether excluded. Sexual isolation is found, as a rule, in interspecific

crosses. Rudiments of sexual isolation have been found also within a species, e.g., in crosses between certain strains of *D. miranda*,[3] *D. sturtevanti* and *D. prosaltans* from Brazil and Guatemala.[2] One-sided mating preferences are known in most geographic races of *D. prosaltans*, in *D. Willistoni*[1] and in *D. nebulosa*. Such mating preferences do not render the gene exchange impossible, because at least one of the two populations would continue to receive an inflow of genes from the other.

Since hybrids between two forms, each of which possesses a well-balanced genotype, may be ill balanced or unfit for survival, reduction or cessation of the gene exchange between populations may be adaptively important. Genetic variants which reduce the rate of the gene exchange may be favored by natural selection in populations exposed to hybridization. Reproductive isolation would be strengthened by natural selection until complete suspension of the gene exchange is attained. The development of all forms of reproductive isolation, including sexual isolation, between populations which have diverged sufficiently to make compromise genotypes unfavorable may be initiated and furthered by natural selection.[4, 5] On the other hand, Muller[6, 7] has pointed out that impediments to gene exchange may arise accidentally, as concomitants of the process of divergence of genetic systems.

These two suggestions may be complementary rather than conflicting. It is well known that natural selection operates with the genetic variants present in populations, but cannot create such variants. The variants are bound to arise, in a sense, accidentally, through mutation and recombination. The one-sided mating preferences of the kind observed in *D. prosaltans* would not, even if the geographic races involved were exposed to hybridization, constitute a barrier to gene exchange. Such mating preferences may, however, serve as raw materials from which true sexual isolation could develop by addition of genetic variants making the aversion to heterogamic matings mutual instead of unidirectional. Incipient sexual isolation is, indeed, found between strains of *D. prosaltans* from Brazil and Guatemala. Incipient sexual isolation is widespread among geographic strains of *D. sturtevanti*, but it is still neither strong enough to be a serious obstacle to gene exchange, nor ordered into a balanced system of isolation correlated with geography. One-sided mating preferences are very likely by-products of physiological racial differences, not necessarily related to the mating reactions. True sexual isolation develops if one-sided mating preferences are added up and coördinated by natural selection.

The great diversity and complexity of structures and habits connected with the search for mates, nest building, courtship and copulation in many groups of animals is very impressive. These structures and habits are often not only surprisingly complex but also constant within and characteristically different between species. Their origin in evolution seems difficult

to explain. Their orderly complexity makes accidental origin extremely improbable. Natural selection would seem to be incapable of building them because of the apparent lack of adaptive value in most of these structures and habits. Darwin's theory of sexual selection was a partially successful attempt to resolve this difficulty, but the competition for mating postulated by the theory is relatively seldom observed. It is, therefore, desirable to keep in mind the possibility that species specific courtship and mating habits and associated structures may serve as "recognition marks" of the specific identity.[8] If so, these habits and structures may possess adaptive value as integral parts of the mechanism of sexual isolation, and for this reason may be developed by a process of selection. Such a modification of the theory of sexual selection would, it seems, avoid most of the difficulties confronted by its original, Darwinian, version.

It should also be kept in mind that the problem of sexual structures and habits which seem to be devoid of adaptive significance is only a part of the broader problem of the origin in evolution of the so-called "neutral" characters in general. It is customary to suppose that neutral characters become established in evolution because of being physiologically correlated with some adaptively important, although less readily perceptible, characters. Unfortunately, the postulated correlations can only seldom be demonstrated to exist. For some neutral characters a reasonable alternative would be to suppose that they function as recognition marks of the species during the courtship and mating processes, and, are, therefore, susceptible of modification and development by selection.

The assistance of Miss Irene Markreich in conducting the experiments is gratefully acknowledged.

Summary.—Geographic strains of *D. sturtevanti* show incipient sexual isolation. The extent of this isolation is, however, variable and is not strictly correlated with the geographic origin of the strains; some strains coming from remote localities show less aversion to interbreeding than strains from less remote localities. The origin in evolution and the biological functions of the sexual isolation proper, as well as of other forms of preferential mating, are discussed.

[1] Dobzhansky, Th., and Mayr, E., these PROCEEDINGS, **30**, 238–244 (1944).
[2] Dobzhansky, Th., and Streisinger, G., *Ibid.*, an article appearing in this issue.
[3] Dobzhansky, Th., and Koller, P., *Biol. Zentr.*, **58**, 589–607 (1938).
[4] Dobzhansky, Th., *Amer. Natur.*, **74**, 312–321 (1940).
[5] Dobzhansky, Th., *Genetics and the Origin of Species*, New York, 1941.
[6] Muller, H. J., *Biol. Reviews*, **14**, 261–280 (1939).
[7] Muller, H. J., *Biol. Symposia*, **6**, 71–125 (1942).
[8] Mayr, E., *Systematics and the Origin of Species*, New York, 1942.

EXPERIMENTS ON SEXUAL ISOLATION IN DROSOPHILA. II. GEOGRAPHIC STRAINS OF DROSOPHILA PROSALTANS

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It has been shown[1] that when males of Brazilian strains of *Drosophila willistoni* are confined with females of their own and of other Brazilian strains, the females are inseminated at random. But when Brazilian or Guatemalan males are kept with mixtures of Brazilian and Guatemalan females, there is a tendency for a greater proportion of the Brazilian than of the Guatemalan females to be inseminated. A more complex system of sexual preferences, which exists within the species *D. prosaltans* Duda (= *D. sellata* Sturtevant), is described in the present article.

Strains of *D. prosaltans* coming from the following localities (Fig. 1) have been used: Huichihuayan, state of San Luis Potosi, Mexico; Chilpancingo and Zopilote Canyon, state of Guerrero, Mexico; Guatemala City, Guatemala; Belem, state of Pará, Brazil; Bertioga and Iporanga, state of São Paulo, Brazil. The strains from Mexico and Guatemala were obtained through the courtesy of Professors J. T. Patterson and A. H. Sturtevant. The Brazilian strains were collected by the senior author. All seven strains intercross readily, produce fertile hybrids, and doubtless belong to the same species. Yet the peculiar chromosome structure found in the South-Brazilian strains (Bertioga and Iporanga)[2] is absent in the strains from Belem, Guatemala and Mexico, which have V-shaped X's and Y's, one pair of V-shaped autosomes, and one pair of rod-like autosomes. Furthermore, in the Mexican strains the basal bands on the abdominal tergites are broader, lighter in color and sharper in outline than those of the Brazilian ones;[3] the Guatemala strain is intermediate in this respect and closer to those from Brazil than to those from Mexico. Finally, under the conditions of the experiments, sexual activity in the Mexican strains starts on the second day and in the Brazilian strains on the third day after hatching from the pupae.

A slight modification of the experimental techniques used for *D. willistoni*[1] was followed in the work with *D. prosaltans*. Ten freshly hatched females of each of two strains—i.e., twenty females in all—are placed in a vial with ten freshly hatched males of one of these strains. The right wings are clipped in one class of females and the left wings in the other, or else in one class a wing is cut and in the other left intact. The vials are kept at 24½°C. for about 3 days, where cultures with Mexican males are concerned, or for 4 days if Brazilian males are used. The females are then

dissected, and their seminal receptacles are examined for sperm. The vials in which too few or too many (less than 20% or more than 80%) of the females are inseminated are discarded (such vials are infrequent). The tubular (ventral) receptacle in *D. prosaltans* is a very long tube, resembling a skein of wool that is folded, as a whole, into the shape of an M. Live spermatozoa lying parallel to the axis of the tube are easily seen. The spherical chitinous spermathecae contain a tangled mass of sperm in which only some moving threads can be seen.[4] If a female is killed while in coitu or shortly thereafter, the spermathecae and all but the proximal gyres of the tubular receptacle are free of sperm, but a viscous ejaculate is found in the vagina.

A summary of the data is presented in table 1. Numbers of the females dissected and percentages of them found inseminated are given for the homogamic (i.e., inseminated by males of the same strain) and the heterogamic (i.e., inseminated by males of the foreign strain) combinations. The χ^2's for the observed differences between the frequencies of the homogamic and the heterogamic matings, and the isolation indices[5] are also included. It is evident at a glance that preferential mating is the rule rather than an exception when different geographic strains of *D. prosaltans* are brought together, and that strong preferences for homogamic matings (positive isolation indices) as well as for heterogamic matings (negative isolation indices) are common. Taking the 0.05 or 0.01 probability levels (corresponding to χ^2's of 3.84 and 6.64) as the limits of significance, we find that 35 or 34 out of the 42 crosses made give results deviating from randomness of mating. Significant positive isolation indices are found in 23 or 24, and significant negative ones in 11 crosses.

The relationships observed can be described most simply as follows. The geographic strains examined form a hierarchic series: Chilpancingo $\geqslant$ Zopilote $>$ Huichihuayan $>$ Guatemala $>$ Belem $>$ Iporanga $\geqslant$ Bertioga. If males of a strain higher up in this series are confined with females of the same strain and of another strain lower down in the series, the frequency of homogamic matings exceeds that of the heterogamic ones, making the isolation index positive. But if males of a "low" strain are kept with a mixture of females of their own and of a "higher" strain, the frequency of heterogamic matings exceeds that of the homogamic ones, and the isolation index is negative. This regularity was found in 36 out of 42 crosses; the exceptions are discussed below.

Chilpancingo males always inseminate more of their own than of foreign females. This preference[6] is very strong in mixtures of Chilpancingo with Bertioga and Iporanga females, a little less strong in mixtures with Belem, Guatemala and Huichihuayan, and least strong in mixtures with Zopilote females. It may seem surprising, however, that, with the exception of the Zopilote males which show no preference, males of all other strains in-

TABLE 1

NUMBERS OF FEMALES DISSECTED (*n*) AND PER CENT CARRYING SPERM (%) IN VARIOUS CROSSES OF *Drosophila prosaltans*

FEMALES	MALES	HOMOGAMIC *n*	HOMOGAMIC %	HETEROGAMIC *n*	HETEROGAMIC %	χ^2	ISOLATION INDEX
Chilpancingo, Zopilote	Chilpancingo	60	88.3	65	60.0	12.8	0.19
Chilpancingo, Zopilote	Zopilote	91	57.1	90	56.7	0.0	0.00
Chilpancingo, Huichihuayan	Chilpancingo	72	95.8	70	32.9	61.7	0.49
Chilpancingo, Huichihuayan	Huichihuayan	48	31.2	47	87.2	30.8	−0.47
Chilpancingo, Guatemala	Chilpancingo	60	96.7	63	28.6	60.7	0.54
Chilpancingo, Guatemala	Guatemala	93	40.9	106	71.7	19.3	−0.27
Chilpancingo, Belem	Chilpancingo	91	89.0	86	26.7	70.5	0.54
Chilpancingo, Belem	Belem	111	27.0	102	74.5	47.9	−0.47
Chilpancingo, Bertioga	Chilpancingo	48	91.7	48	6.2	70.0	0.87
Chilpancingo, Bertioga	Bertioga	103	17.5	111	65.8	51.0	−0.58
Chilpancingo, Iporanga	Chilpancingo	57	100.0	57	14.0	85.9	0.75
Chilpancingo, Iporanga	Iporanga	85	35.3	89	67.4	18.0	−0.31
Zopilote, Huichihuayan	Zopilote	71	71.8	72	34.7	19.7	0.35
Zopilote, Huichihuayan	Huichihuayan	105	26.7	114	69.3	39.7	−0.44
Zopilote, Guatemala	Zopilote	65	75.4	59	18.6	40.1	0.60
Zopilote, Guatemala	Guatemala	67	28.4	75	58.7	13.0	−0.35
Zopilote, Belem	Zopilote	46	95.6	42	26.2	45.5	0.57
Zopilote, Belem	Belem	112	49.1	113	61.1	3.2	−0.11
Zopilote, Bertioga	Zopilote	77	72.7	76	19.7	43.3	0.57
Zopilote, Bertioga	Bertioga	105	32.4	108	67.6	26.4	−0.35
Zopilote, Iporanga	Zopilote	50	92.0	53	32.1	38.8	0.48
Zopilote, Iporanga	Iporanga	82	26.8	80	70.0	30.1	−0.45
Huichihuayan, Guatemala	Huichihuayan	92	71.7	92	38.0	21.1	0.31
Huichihuayan, Guatemala	Guatemala	79	36.7	80	48.7	2.6	−0.14
Huichihuayan, Belem	Huichihuayan	86	77.9	82	13.4	70.1	0.71
Huichihuayan, Belem	Belem	106	57.5	100	30.0	15.8	−0.31
Huichihuayan, Bertioga	Huichihuayan	74	58.1	74	17.6	25.8	0.54
Huichihuayan, Bertioga	Bertioga	100	32.0	96	51.0	7.1	−0.23
Huichihuayan, Iporanga	Huichihuayan	76	81.6	75	48.0	18.7	0.26
Huichihuayan, Iporanga	Iporanga	100	33.0	95	45.3	3.1	−0.16
Guatemala, Belem	Guatemala	103	55.3	102	10.8	46.5	0.67
Guatemala, Belem	Belem	99	55.6	106	16.0	35.0	0.55
Guatemala, Bertioga	Guatemala	51	64.7	51	11.8	30.2	0.69
Guatemala, Bertioga	Bertioga	78	66.7	80	41.3	10.2	0.24
Guatemala, Iporanga	Guatemala	50	60.0	52	11.5	26.2	0.68
Guatemala, Iporanga	Iporanga	164	60.4	155	38.7	14.9	0.22
Belem, Bertioga	Belem	122	53.3	116	36.2	7.0	0.19
Belem, Bertioga	Bertioga	91	41.8	94	21.3	9.1	0.32
Belem, Iporanga	Belem	94	45.7	94	50.0	0.3	−0.04
Belem, Iporanga	Iporanga	85	43.5	80	41.2	0.1	0.03
Bertioga, Iporanga	Bertioga	70	42.8	67	38.8	0.2	0.05
Bertioga, Iporanga	Iporanga	99	61.6	108	48.1	3.8	0.12

seminate Chilpancingo females in preference to females of their own strains. The preference is exhibited most strongly by males from Bertioga, which give a negative isolation index as low as -0.58.

Zopilote flies are about equivalent to Chilpancingo, but the positive as well as the negative isolation indices tend to be lower where Zopilote flies are concerned. Huichihuayan males prefer their own females to those of Guatemala, Belem, Bertioga and probably Iporanga, but inseminate Chilpancingo and Zopilote females in preference to their own. Hiuchihuayan females placed with Chilpancingo and Zopilote are discriminated against by males of the latter strains, but are preferred by Guatemala, Belem, Iporanga and Bertioga males in the presence of their own females.

Guatemala and Belem strains behave somewhat differently from those discussed above. As might be expected from the position of the Guatemala strain in the hierarchic series, Guatemala males inseminate their own females preferentially in mixtures with Belem, Bertioga and Iporanga, but prefer foreign females in mixtures with Chilpancingo, Zopilote and probably Huichihuayan. But Guatemala females are not inseminated by males of any strain in preference to females of their own strain. Belem, Bertioga and Iporanga males, which stand lower in the hierarchic series than Guatemala, inseminate a greater proportion of their own than of Guatemala females; Chilpancingo, Zopilote and Huichihuayan males do likewise. There is, consequently, a true sexual isolation—that is, a reciprocal aversion—between the Guatemala and the Brazilian strains, and if flies from Guatemala and Brazil were mixed the matings would be mostly homogamic. As shown above, there is no reciprocal aversion between Guatemala and Mexican strains, or between Mexican and Brazilian strains, Mexican females being always preferred. The Belem strain seems to behave in a manner similar to the Guatemala. In accordance with the position of this strain in the hierarchy, Belem males give negative isolation indices in mixtures with Mexican and their own females, but positive isolation indices in mixtures with Bertioga females. However, Bertioga males placed with Bertioga and Belem females inseminate the former preferentially. Matings occur more or less at random in mixtures of Belem and Iporanga, or of Bertioga and Iporanga flies.

The hierarchy of sexual preferences of strains of *Drosophila prosaltans* is clearly correlated with the geographic origin of these strains (Fig. 1). The three highest strains all come from Mexico, which is the northern limit of the distribution area of the species. The two lowest strains are from southern Brazil, and the intermediate strains from Central America and from equatorial Brazil. Strains from localities geographically close to each other are more or less similar (Chilpancingo and Zopilote, Iporanga and Bertioga).

The discovery of negative isolation indices, which signify that matings

between representatives of different strains are more frequent than between those of the same strain, was unexpected. Since sexual activity starts sooner after hatching of the flies from the pupae in Mexican than in

FIGURE 1

A map showing the localities in which strains of *D. prosaltans* and *D. sturtevanti* have been collected.

Brazilian strains, it seemed possible that the results obtained in our experiments, in which flies of the same chronological age are placed together, reflected merely the difference in biological age of the flies. Indeed, females

may become more sexually receptive as they grow older, and therefore older females may be inseminated in preference to younger ones. To test this possibility, Brazilian females were kept for two days on abundant food but without males, and then placed in vials with freshly hatched Mexican females and freshly hatched males of either kind. The females were dissected and examined as usual. The results are summarized in table 2. The rate of insemination clearly does not depend upon the age of the females alone, although the isolation indices in table 2 are lower than those for the corresponding crosses in table 1.

TABLE 2

NUMBERS OF FEMALES DISSECTED (*n*) AND PER CENT CARRYING SPERM (%) IN CROSSES IN WHICH BRAZILIAN FEMALES WERE OLDER THAN THE MEXICAN ONES

FEMALES	MALES	HOMOGAMIC *n*	HOMOGAMIC %	HETEROGAMIC *n*	HETEROGAMIC %	χ^2	ISOLATION INDEX
Chilpancingo, Bertioga	Chilpancingo	133	80.5	136	25.7	80.8	0.52
Chilpancingo, Bertioga	Bertioga	69	34.8	71	66.2	13.8	−0.31
Chilpancingo, Belem	Belem	41	53.7	40	80.0	5.3	−0.20

Summary.—The strains of *D. prosaltans* form a graded series with respect to their sexual preferences, and this seriation corresponds in a general way to the geographic origin of these strains. When northern (Mexican) males are kept with a mixture of northern and southern (Brazilian) females, more of the former than of the latter are inseminated. In similar experiments, the southern males also inseminate more northern than southern females. Females of the strains from Guatemala and from equatorial Brazil are discriminated against by South-Brazilian males in favor of females from the South-Brazilian strains.

[1] Dobzhansky, Th., and Mayr, E., these PROCEEDINGS, **30**, 238–244 (1944).

[2] Dobzhansky, Th., and Pavan, C., *Ibid.*, **29**, 368–375 (1943).

[3] This external difference is not sufficient to distinguish the Mexican and the South-Brazilian flies in all cases. Young Mexican flies have the same "faded-out" appearance as the older Brazilian flies, the "bright" coloration characteristic of the Mexican race developing only gradually with age. It does not seem advisable at this time to recognize the Mexican race taxonomically by attaching to it a Latin name.

[4] This condition, and the fact that the opening of the spermathecal duct is provided with a brush of chitinous needles protruding into the cavity of the spermatheca, suggests that the sperm stored in it is not used in fertilization of eggs. It seems possible that the function, in Drosophila, of the sperm in the chitinous spermathecae is to stimulate the development of the eggs in the ovary through a hormone-like mechanism.

[5] Stalker, H. D., *Genetics*, **27**, 238–257 (1942).

[6] It should be stressed that expressions like "preference" and "discrimination" are used merely to avoid circumlocutions. Our data show merely the frequencies of insemination of females of different strains, and it is not known whether these frequencies depend upon the behavior of males, of females or of both sexes.

MENDELIAN INHERITANCE OF ADAPTIVE ENZYMES IN YEAST*

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Introduction. Our previous analysis[1, 2] of the mechanism of galactozymase production in *Saccharomyces cerevisiae* revealed that it is an adaptive[3] enzyme. The existence of unadaptable strains indicated that the initiation of enzyme synthesis was genetically controlled. The adaptation time for each specific strain was reproducible under standard conditions. While the genetic composition determines the initiation of enzyme synthesis, the quantitative level of enzyme in the cell below the maximum depends on an interaction between the specific fermentable substrate and the cytoplasm. It was thus of some interest to examine the adaptability of the progeny of two species differing in the possession of an adaptive enzyme.

S. validus and S. mandshuricus both possess the ability to ferment melibiose. Hybrids between these forms and other fermenting and non-fermenting yeasts led Winge and Laustsen[4] to state that "the presence of a specific enzyme is dominant to its absence in all the instances studied." They made matings by placing two spores in contact with each other. This method has the disadvantage that one cannot characterize the haplophase parents since both of the original spores are consumed in the mating. Furthermore, the genetical mechanism was not analyzed, since the phenotypes of the segregants from the hybrids were not examined. Finally, as will be shown here, melibiozymase is an adaptive enzyme, hence Winge and Laustsen's observations concerning the dominance of fermentative capacity need not imply a genetic basis. It is conceivable that hybrids of fermenting by non-fermenting strains may all be fermenters simply because they all carry 50% fermenting type cytoplasm (with its enzymes).

In the present experiments, the progeny of a hybrid between *S. carlsbergensis* and *S. cerevisiae* and other related progenies were examined. *S. carlsbergensis* can adapt to melibiose fermentation while *S. cerevisiae* cannot. The hybrids were produced by mixing haplophase cultures according to a method recently described.[5, 6, 7] Since only part of the culture is needed for the mating, the remainder can be used to determine the characteristics of the parent strain. Portions of the clone-culture are also available for back-crossing or mating to other clones of interest.

Methods.—One liter of the basic medium contained the following substances: 2 g. autolyzed yeast extract powder, 3 g. Bactopeptone, 1 g.

$(NH_4)_2SO_4$, 0.133 g. K_2PO_4, 1.866 g. KH_2PO_4, 0.25 g. $MgSO_4$, 0.125 g. $CaCl_2$, 1 cc. of 50% sodium lactate. Eight per cent cerelose was added to grow crops of yeast for adaptability test. Solid medium was made by adding 30 g. of agar to the above. A 12% solution of Eastman melibiose containing less than 0.01% of other fermentable carbohydrate was sterilized by Seitz filtration and added to the basic (carbohydrate free) medium to produce a solution containing 4% melibiose.

Test for Ability to Ferment Melibiose.—All 175 cultures were characterized according to their ability to ferment melibiose by the standard inverted tube technique. These tests were run in duplicate and over 90% of the cultures were held for a period of more than 30 days when the results were recorded. Many repetitions were made, also in duplicate, with uniformly identical results. The presence or absence of gas production is recorded in figure 2 by the signs + and −.

In using the inverted tube method, part of a clone is seeded into the broth containing melibiose as the carbohydrate source and allowed to grow. Since every mutation in a haplophase population becomes functional immediately, a positive test might not mean that the original clone possessed the fermentative capacity. Selection of a mutant produced during growth in the melibiose solution may have occurred. To exclude this possibility, these data were supplemented by duplicate tests of 12 critical cultures using Warburg manometers. A portion of the original clone was seeded into ordinary cerelose broth. After 48 hours' incubation, the resultant growth was centrifuged and washed twice with $M/15$ KH_2PO_4. It was then resuspended in $M/15$ KH_2PO_4. Melibiose was added in sufficient amounts to make a 4% solution. Under these conditions, selection is ruled out since no division takes place during the exposure to melibiose. If a stationary population exposed to melibiose acquires the ability to ferment the sugar, it can only be due to an interaction between the existing cells and the sugar. Samples were taken at intervals and tested for the ability to evolve CO_2 under anaerobic conditions. Fresh melibiose was always added to the suspension at the beginning of each determination to insure the presence of excess substrate.

It is highly improbable that a growing haplophase population kept in contact with cerelose (glucose) will acquire the ability to ferment melibiose because conditions would act against the selection of a melibiose-fermenting mutant. However, it is conceivable that a haplophase culture capable of fermenting melibiose grown for a long time on glucose might lose the ability to ferment melibiose by the selection of a non-fermenting mutant. There were no instances of this type during the present study, indicating that the melibiose fermenting genes are very stable. In all cases the results obtained with the manometric method agreed with those yielded by the inverted tube procedure.

Adaptation Times.—For accurate determinations of adaptation times, it was found[8] that the R. Q., which could be followed continuously by the two vessel method,[9] could be used. When the R. Q. reached a value of 1.8, the culture was considered adapted since this meant a $Q^{N}_{CO_2}$ value of 100. This was checked by flushing the KOH free cup with nitrogen after the R. Q. had exceeded 1.8 and measuring the $Q^{N}_{CO_2}$ value. All measurements were taken at 30.2°C., the temperature at which the suspensions were incubated with the substrate. The vessels were shaken at a rate of 100 oscillations per minute over a 7-cm. arc. The nitrogen used to displace the air in measurements of anaerobic CO_2 production was passed over hot copper to remove any traces of oxygen.

The Adaptive Nature of the Melibiose-Fermenting Enzyme.—To determine whether or not *S. carlsbergensis* is able to ferment melibiose immediately

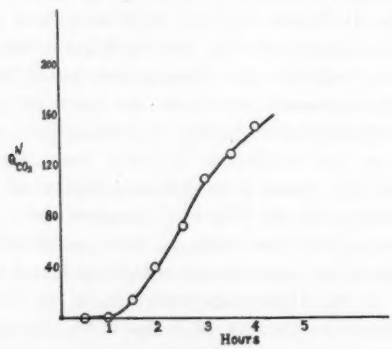

FIGURE 1

Graph showing adaptive nature of melibiose fermentation by *S. carlsbergensis.*

or only after a period of adaptation, phosphate suspensions of 48-hour, cerelose-grown cultures were placed in Warburg vessels with melibiose in the sidearms. After flushing with nitrogen, the melibiose was tipped. In no case was CO_2 evolved immediately or subsequently within 8 hours. However, if similarly prepared suspensions were incubated in air in the presence of melibiose and samples tested at intervals for anaerobic CO_2 evolution, measurable rates were found within 100 minutes, indicating that the enzyme-system necessary for melibiose fermentation is formed rapidly only after aerobic incubation in the presence of the substrate.

Figure 1 gives a representative curve of $Q^{N}_{CO_2}$ values after various periods of incubation. Four such tests were made in duplicate of the original cultures of *S. carlsbergensis* with the same results. Eight separate determinations of the adaptation times of this culture were made and an average

value of 167 ± 10 minutes was obtained. It is clear from these experiments that the ability to ferment melibiose involves the formation of an

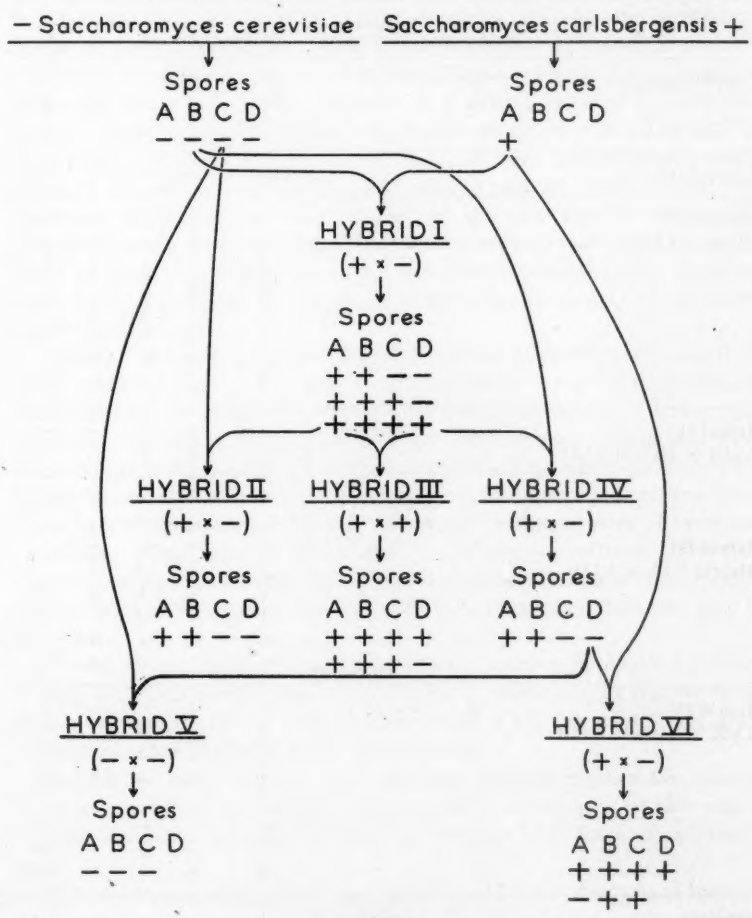

FIGURE 2

Fermentation of melibiose by diploid and and haploid progeny of *Saccharomyces cerevisiae* by *S. carlsbergensis* hybrids.

adaptive enzyme. It differs in no essential way from the galactozymase activity previously studied. As in the case of galactose fermentation, cells which have been adapted to ferment melibiose lose this ability when removed from the substrate and have to be readapted to use it fermenta-

TABLE 1

FERMENTATION OF MELIBIOSE BY PROGENY OF VARIOUS CROSSES BETWEEN *Saccharomyces cerevisiae* (MELIBIOSE −) BY *Saccharomyces carlsbergensis* (MELIBIOSE +)

DIPLOID	PHENOTYPE OF DIPLOID	PHENOTYPES OF COPULANTS	NO. OF ASCUS	SPORE A	SPORE B	SPORE C	SPORE D
S. carlsbergensis	+		C1	+			
			C5	+	+	+	+
			C6	+	+	+	+
S. cerevisiae	−		Lk5	−	−	−	−
Hybrid I	+	− x +	1	+	+	+	+
(Lk5B × C1A)			2	+	+	+	+
			3	+	+	+	+
			4	+	+	−	+
			5	+	+	+	
			6	+	−	+	+
			7	+	−	+	
			8	+	−	+	−
Hybrid II	+	− x +	1	+	+	−	−
(Lk5B × Hybrid I-1A)			2	+	−	+	
			3	+	−	+	−
			4	−		+	−
Hybrid III	+	+ × +	1	+	+	−	
(Hybrid I-1A × I-1D)			2	+	+	+	
			3	+	+	+	+
			4	+	−	+	+
			5	+	+	+	
			6		+	+	+
Hybrid IV	+	− × +	1	+		−	−
(Lk5C × Hybrid I-1D)			2	+	−		
			3	−	−	+	
			4	+	−	+	−
			5			−	+
			6		−		+
			7	−	+	+	−
			8	+	+	−	−
Hybrid V		− × −	1	−	−	−	
(Lk5C × Hybrid IV-7D)			2	−	−	−	
Hybrid VI	+	+ × −	1	+	+	+	+
(C1A × Hybrid IV-7D)			2	−	+	+	

Four spores were removed from each ascus and designated arbitrarily as *A*, *B*, *C*, *D*.

Pluses and minuses in these columns indicate that the spores, respectively, fermented or failed to ferment melibiose.

A blank space indicates that the spore failed to produce a viable colony.

tively. This adaptive behavior was true not only of the original *S. carlsbergensis*, but of all the haploid and diploid progeny which were tested, although the adaptation times varied. Wherever a clone is indicated as positive, it only showed that character after aerobic incubation in the presence of melibiose. None could ferment it on immediate contact.

Mendelian Segregation of the Adaptive Enzyme.—Figure 2 is a pedigree indicating the characteristic progeny of a hybrid between *S. cerevisiae* (mel −) and *S. carlsbergensis* (mel +), which are listed in detail in table 1. Four single ascospore cultures (Lk5A, B, C, D) were isolated from a single ascus of *S. cerevisiae*. Each one was haploid and all failed to adapt to melibiose fermentation. Several asci of *S. carlsbergensis* were also dissected, but in these early experiments only one spore per ascus survived. Each of these was adaptable. Two asci from *S. carlsbergensis* dissected later, gave eight cultures (C5A, B, C, D, and C6A, B, C, D) each of which proved adaptable.

Hybrid I was an interspecific hybrid (*cerevisiae by carlsbergensis* Lk5B × C1A) made by mixing melibiose + and melibiose − haplophase cultures. Three diploid cells isolated from this culture were all capable of fermenting melibiose, confirming the results of Winge and Laustsen. Eight asci were dissected from the interspecific hybrid and all the haplophase progeny were tested for the ability to ferment melibiose. The haplophase cultures from three asci all fermented melibiose. Two asci produced three + and one − culture. One ascus produced two + and two − cultures. The fact that in some cases more than two of the haplophase segregants from a single diploid nucleus fermented melibiose indicates that more than one gene is involved.

Hybrid II was produced by back-crossing positive haplophase culture I-1A to a negative haplophase culture from *S. cerevisiae*. A regular Mendelian segregation of the progeny shows that I-1A carries a single gene capable of controlling melibiose fermentation.

Hybrid IV was made by back-crossing positive haplophase culture I-1D to a negative haplophase culture from *S. cerevisiae*. In this case a regular Mendelian segregation again shows that a I-1D also carries a single gene.

Hybrid III was produced by mating I-1A by I-1D. Analysis of hybrids II and III has proved that each of these cultures carries a single gene controlling melibiose fermentation. If these genes are alleles, all the haplophase progeny of the hybrid should ferment melibiose. Two of the 20 haplophase segregants failed to ferment melibiose, proving that the gene carried by I-1A is not an allele of the gene carried by I-1D. Therefore, the original culture of *S. carlsbergensis* contained two different non-allelic loci controlling melibiose fermentation.

Hybrid V was made by back-crossing negative haplophase IV-7D to a

negative haplophase from *S. cerevisiae*. Six haplophase progeny from two asci were all negative.

Hybrid VI was made by back-crossing the same culture (IV-7D) to a positive haplophase of *S. carlsbergensis*. Six of seven haplophase progeny fermented melibiose, while one failed. This finding together with the results obtained in Hybrid V confirms the fact that C1A possesses two genes controlling melibiose fermentation.

Summary and Conclusions.—*S. carlsbergensis* and its haploid segregants can adapt to melibiose fermentation while *S. cerevisiae* and its haplophase progeny cannot. Data obtained from 175 progenies of the interspecific and of related hybrids are consistent with the view that *S. carlsbergensis* contains two pairs of dominant genes, each of which controls the production of an adaptive enzyme. The gene initiates the synthesis of a melibiose fermenting enzyme complex, providing melibiose is present. *S. cerevisiae* is homozygous for the recessive alleles.

* Aided by a grant from Anheuser-Busch, Inc., St. Louis, Mo.

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[3] Karstrom, J., *Ergeb. Enzymforsch.*, **7**, 350–376 (1937).

[4] Winge, O., and Laustsen, O., *Compt. rend. travaux lab. Carlsberg, série physiologique* **22**, 337–352 (1939).

[5] Lindegren, C. C., and Lindegren, G., these PROCEEDINGS, **29**, 306–308 (1943).

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[7] Lindegren, C. C., and Lindegren, G., *Jour. Bact.*, **46**, 405–419 (1943).

[8] Spiegelman, S. in ms.

[9] Dixon, M., *Manometric Methods*, Cambridge, 1934, 122 pp.

APOMIXIS IN GUAYULE

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The literature on the morphology of reproduction in guayule (*Parthenium argentatum* Gray) indicates that many irregularities occur in the development of the seed in this species. Thus Kirkwood[1] observed no division of the megaspore mother cell but in some preparations he found "what appeared to be vestiges of a non-functional spore." He suggested, therefore, that, at the most, the megaspore mother cell divided once before the 8-nucleate embryo sac was formed in the "usual manner." In her studies on the female gametophyte of guayule, Kokieva[2] listed a series of features that are usually taken as indications of parthenogenesis;

however, she was unable to prove that this phenomenon occurred in guayule. Dianowa, *et al.*,[3] also denied the existence of parthenogenesis in *P. argentatum* and other species of this genus.

The plants of *P. argentatum* that were used in the present study were of the 36- and 72-chromosome types. (Details regarding the origin of this material are to be published later.) The development of the female gametophyte and embryo differed in relation to the chromosome numbers. The 36-chromosome plants were largely, if not entirely, sexual; the 72-chromosome material was predominantly apomictic.

Table 1 illustrates the difference between the 36- and the 72-chromosome types with regard to the early development of the embryo sac. The figures in this table are based on an examination of young ovules ranging from 70 to about 400 microns in height. The youngest ovules showed megaspore mother cells enclosed within a nucellus that was still protruding beyond the integument; the oldest ovule was one with a tetranucleate embryo sac associated with a disintegrated nucellus and with an integument that completely enclosed the embryo sac and projected beyond it in the micropylar region.

The 36-chromosome material showed many megaspore mother cells in different stages of meiosis (item 3, table 1). Dyad and tetrad formation followed meiosis (items 5 and 6, table 1). Most of the uninucleate embryo sacs and many of the binucleate ones were associated with crushed megaspores. Sooner or later after the enlargement of the functioning megaspore the nucellus was destroyed. In the 72-chromosome material the high percentage of megaspore mother cells (items 2 and 3, table 1) and particularly of resting megaspore mother cells (item 2, table 1) indicated that the gametophyte formation proceeded slowly. The megaspore mother cells were of different sizes; some were so much enlarged that they were comparable to the uninucleate embryo sacs and were associated with a crushed nucellus (item 4, table 1). Views showing tetrads or crushed megaspores were few.

The occurrence of the relatively large, uninucleate structures associated with no crushed megaspores, but frequently with a disorganizing nucellus indicates omission of meiosis; conversely, the presence of megaspores (whether degenerating or not) is an evidence of preceding meiosis.[4] Judging by the items 4 to 6 in table 1 omission of meiosis is rare in the 36-chromosome plants used in this study but is common in the 72-chromosome plants. This evidence is strengthened by the observation that most of the megaspore mother cells in the 36-chromosome material were in some stage of meiosis, whereas most of those in the 72-chromosome plants were resting (items 2 and 3, table 1).

Thus apomixis in guayule involves *apomeiosis* of the type of *generative apospory*,[5] in which the megaspore mother cell does not form tetrads but

directly develops into a uninucleate embryo sac with a diploid number of chromosomes. Since the apomictic 72-chromosome material showed some meiosis also the apospory in guayule may be termed *facultative*. Kirkwood[1] apparently noted this phenomenon in guayule but did not realize the significance of his observation.

The percentage of apospory in the 72-chromosome material can be roughly estimated from items 1 to 7 of table 1. Items 2 and 4 may be taken as indications of apospory and items 3 and 5 to 7 as evidences of meiosis. (Some of the megaspore mother cells in item 2 would probably have undergone meiosis; on the other hand, not all divisions in item 3 were identified as meiotic.) With these assumptions there was 74.2% of apospory in the 72-chromosome material. This figure agrees well with the percentages of maternal types (61.6 to 95.2%) that were observed by Powers and Rollins[6]

TABLE 1

COMPARISON OF THE 36- AND 72-CHROMOSOME TYPES OF GUAYULE PLANTS WITH REGARD TO EMBRYO-SAC FORMATION

ITEM NUMBER	DESCRIPTION OF THE ITEM	36-CHROMOSOME TYPE	72-CHROMOSOME TYPE
1	Number of ovules examined	75	400
2	Per cent of resting megaspore mother cells	1.3	55.5
3	Per cent of dividing megaspore mother cells	21.4	12.0
4	Per cent of "uninucleate embryo sacs"[a] with disintegrating nucellus and no crushed megaspores	1.3	7.8
5	Per cent of dyads	5.4	1.7
6	Per cent of tetrads of megaspores	34.6	7.0
7	Per cent of uninucleate embryo sacs with crushed megaspores	8.0	1.3
8	Per cent of binucleate embryo sacs	8.0	12.2
9	Per cent of tetranucleate embryo sacs	20.0	1.8
10	Per cent of degenerated embryo sacs	0	0.7

[a] These are enlarged megaspore mother cells.

in the F^1 generations of several *P. argentatum* Gray ♀ × *P. incanum* H.B.K. ♂ crosses. The same authors found no such apomictic reproduction when 36-chromosome plants were used as female parents and the present data suggest less than 4% apospory in similar plants.

Generative apospory leads to the formation of an "unreduced gametophyte" with a diploid egg cell capable of giving rise to an embryo without fertilization. The occurrence of such embryo formation in guayule was checked by comparing pollinated and non-pollinated material from 36- and 72-chromosome plants. (The emasculations and pollinations were carried out by Dr. Reed C. Rollins of the Special Guayule Research Project, U.S.D.A.) The achenes from the non-pollinated flowers of a 36-chromosome plant contained no embryos; open pollinated plants of the same type contained embryos, usually associated with developing endo-

sperm. Non-pollinated 72-chromosome plants contained embryos in most ovules, but the lack of pollination reduced the percentage of ovules in which the endosperm was developing and either reduced or completely inhibited the development of full-size embryos. In the pollinated and non-pollinated 72-chromosome plants there was a distinct lack of relationship between the early development of the embryo and that of the endosperm. The morphologic evidence on the beneficial effect of pollination upon embryo and endosperm development in the 72-chromosome material agrees with the data of Powers and Rollins[6] showing that pollination is necessary for the production of viable seed in the apomicts of guayule. The obvious conclusion is that in conjunction with the generative apospory *unreduced pseudogamy*[5] occurs in the apomictic types of guayule.

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A METHOD IN RATIONAL DIOPHANTINE ANALYSIS

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1. The method furnishes rational solutions of a rational diophantine system when such solutions exist. By rational substitutions the system is reduced to a multiplicative system, which is completely solvable either in integers or in rational numbers. If the substitutions are birational, the complete integer or rational solution of the original system is obtained. When the substitutions are not rationally reversible, the method furnishes a partial solution of the original system; and this solution is rational in a certain necessary and sufficient number N of independent free parameters, the number being determined by the system. The obvious geometrical analog is the parametrization of a rational variety in space of a given number of dimensions; and the necessary and sufficient number N' of independent parameters is readily determined in any particular instance. That the arithmetical problem may be radically different from its geometric analog is suggested by the fact that, except in almost trivial systems, $N \neq N'$. For example, N' may be 9 while the corresponding N may exceed 40 million.

Although partial solutions are scarcely in the modern spirit of diophantine analysis, they sometimes imply by-products of interest in other parts of the theory of numbers. To cite an older instance, S. Ryley's[1] striking theorem (1825) that every rational number is a sum of three rational cubes, appears as a consequence of a partial solution of a very special ternary cubic diophantine equation. Geometrical considerations[2] have accounted for the success of Ryley's ingenious devices, which amount algebraically to the rational substitutions mentioned above. Actually, the special ternary cubic equation in question is replaced by a multiplicative system, whose complete solution is obtainable by the present method. But this solution is not the complete solution of the original equation, as the multiplicative system is not equivalent to the equation, an auxiliary restriction being introduced in order to reduce the equation to the multiplicative type. Similarly in all applications of the method to mixed additive and multiplicative systems; and the chief interest of the necessarily incomplete solutions is probably in their possible by-products. The method proposed is general and strictly elementary, and may be regarded as an alternative for the more recent applications of algebraic geometry to the arithmetic of rational varieties. It will suffice here to illustrate it by two examples, of which the first is the ternary cubic equation underlying Ryley's theorem.

2. To solve

$$(\xi + \eta + \zeta)^3 - d\xi\eta\zeta = m$$

in rational numbers ξ, η, ζ, where d, m are given rational numbers, the equation is reduced to the multiplicative type by assuming that $d\xi\eta\zeta + m$ is a product of linear homogeneous functions of the indeterminates ξ, η, ζ. This is equivalent to adjoining an auxiliary equation. A sufficient adjunction (one of an infinity) is essentially Ryley's,

$$d\eta\zeta^2 = m,$$

which reduces the equation to the multiplicative type

$$d\eta\zeta(\xi + \zeta) = (\xi + \eta + \zeta)^3,$$

which is of the form

$$dxyz = u^3.$$

For simplicity let d, m be integers. (If d, m are merely rational, the multiplicative equation is of the type $axyz = bu^3$ with a, b integers such that $(a, b) = 1$. The resolution is similar to that of the equation discussed, but the intermediate formulae involve more parameters.) The complete solution of the multiplicative equation is found in the usual way:

$$x = ay_1z_1x_1^2x_2^2x_3^3,$$

$$y = bx_2z_2y_1^2y_2^2y_3^3,$$

$$z = cx_1y_2z_1^2z_2^2z_3^3,$$

$$u = px_1x_2x_3y_1y_2y_3z_1z_2z_3,$$

in which the letters with suffixes are free parameters, and

$$a \equiv d_4d_6d_8d_3^2t,$$

$$b \equiv d_5d_6d_9d_1^2t,$$

$$c \equiv d_4d_5d_7d_2^2t,$$

$$p \equiv d_1d_2d_3d_4d_5d_6d_7d_8d_9d_{10}t$$

in which t is a free parameter and $d_1, \ldots, d_{10}$ are any integers such that

$$d = d_1d_2d_3d_4d_5d_6d_7^2d_8^2d_9^2d_{10}^3.$$

For given d the number of sets $(d_1, \ldots, d_{10})$ is finite and all sets may be found non-tentatively by solving a set of linear equations. With the above values of x, y, z we have

$$\xi + \eta + \zeta = u,\ \eta = x,\ \zeta = y,\ \xi + \zeta = z;$$

whence $\xi = z - y$, $\eta = x$, $\zeta = y$, subject to the condition

$$x + z = u.$$

The auxiliary equation is now

$$dxy^2 = m.$$

Values of the free parameters in x, y, z must be chosen so that the last two equations have rational solutions for two of the parameters in terms of the others. In this particular instance, z_1, z_2 are given immediately in the required form. (When such is not the case, if any of the parameters in the solution of the multiplicative equation occur with coprime exponents, an obvious replacement of these parameters by suitable powers of themselves, reduces the equation of condition and the auxiliary equation to the present special case.) On substituting the values of z_1, z_2 thus obtained into x, y, z, u, and then the resulting values into the expressions $\xi = z - y$, etc., for ξ, η, ζ we get a rational parametric solution of the given ternary cubic.

The solution may be greatly simplified by absorption: if certain of the parameters appear only as the same function of themselves wherever they occur, this function is no more general than a single free parameter, and may be replaced by one parameter. Here the absorption $x_1x_2^2x_3^2y_1^2y_2^3 \equiv \mu$

and the change in notation $z_3 \equiv \lambda$ followed by the substitution of $\mu\theta$ for λ, where μ, θ are free parameters, gives the solution in the form

$$D \equiv a^2b^2d + cm\theta^3,$$

$$\xi = (m^2p^6\theta^6 - D^3)/abdp\theta D^2,$$

$$\eta = ma^2b^2dp^2\theta^2/D^2,$$

$$\zeta = D/abdp\theta,$$

where d, m are the given (integer) constants of the equation, and a, b, c, p are as stated above. For each set $(d_1, \ldots, d_{10})$ there is a solution ξ, η, ζ, and the number of such sets is finite. The identity $abcd = p^3$ is useful in verifying the solution.

The simplest set of values for the d_j is $d_1 = d$, $d_i = 1$, $i > 1$. For these $a = t$, $b = d^2t$, $c = t$, $p = dt$. Hence, with $t = \phi\theta$, there is the special solution

$$F \equiv d^5\phi^3 + m;$$

$$\xi = (m^2d^6\phi^3 - F^3)/d^4\phi^2F^2,$$

$$\eta = md^7\phi^4/F^2,$$

$$\zeta = F/d^4\phi^2,$$

in which ϕ is a free parameter.[3]

3. The auxiliary equation reducing a given equation to the multiplicative type may render the equation algebraically reducible. Thus

$$(x + y)(y + z)(z + x) - dxyz = m,$$

with the auxiliary equation $m = dyz^2$ reduces the given equation to

$$y^2 + (x + az)y + xz = 0, \qquad a \equiv 1 - d,$$

on discarding a factor which yields only trivial solutions. For rational solutions, it is necessary and sufficient that the y-discriminant of this equation be a square,

$$(x + az)^2 - 4xz = w^2.$$

The last is a multiplicative equation,

$$(x + az + w)(x + az - w) = 4xz,$$

of which a particular solution is given by

$$x + az + w = 2\alpha\theta, \qquad x = \alpha\phi,$$

$$x + az - w = 2\beta\phi, \qquad z = \beta\theta,$$

with α, β, θ, ϕ free parameters. There are thus two solutions,

$$w = (\alpha^2 - 2\alpha\beta + a\beta^2)\theta/(\alpha - \beta),$$
$$x = \alpha(\alpha - a\beta)\theta/(\alpha - \beta),$$
$$z = \beta\theta,$$
$$y = -\beta\theta(\alpha - a\beta)/(\alpha - \beta), \text{ or } -\alpha\theta.$$

Imposing the auxiliary restriction on either of these, we get the rational solution of the original equation,

$$x = -m(m + ad\theta^3)d\theta^2(m + d\theta^3),$$
$$y = m/d\theta^2,$$
$$z = \theta,$$

in which $a \equiv 1 - d$ and θ is a free parameter.

[1] Dickson, L. E., *History of the Theory of Numbers*, Vol. 2, 1920, pp. 726–729.

[2] Richmond, H. W., *Proc. Lond. Math. Soc.*, **21** (2), 401–409 (1922); *Jour. Lond. Math. Soc.*, **17**, 196–199 (1942). Mordell, L. J., *Ibid.*, 194–196. Richmond's papers contain references to the history.

[3] This solution appears to be distinct from those in the literature. However, it is not always easy to prove that formally distinct parametric solutions are numerically distinct.

GROUPS INVOLVING A SMALL NUMBER OF SETS OF CONJUGATE OPERATORS

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The identity constitutes a set of conjugate operators of every group. If a group G involves only one other set of conjugate operators all of its other operators are of the same order and hence it is a prime power group. Such a group always involves at least one invariant operator besides the identity and hence it results that G is then of order 2. If G contains three and only three sets of conjugate operators and is abelian it is the group of order 3. If it is non-abelian it cannot be a prime power group because a group of order p^m, p being a prime number contains at least $p^2 + p - 1$ sets of conjugate operators whenever it is non-abelian, as we proceed to prove.

Suppose that G is a non-abelian group of order p^m, p being an arbitrary prime number. The central quotient group of G is known to be non-cyclic

and hence it is at least of order p^2, and the central of G is known to be at least of order p. If the central of G is of order p and the central quotient group of G is of order p^2 then each of the non-invariant operators of G is commutative with exactly p^2 operators of G and the number of these non-invariant operators of G is $p^3 - p$. The number of the sets of conjugate non-invariant operators of G is therefore $p^2 - 1$ and the number of the sets of conjugates of the invariant operators of G is p, therefore the number of the sets of conjugate operators of G is then $p^2 + p - 1$.

It has now been proved that every non-abelian group of order p^3, p being a prime number, contains exactly $p^2 + p - 1$ sets of conjugate operators. We proceed to prove that every other non-abelian group of order p^m contains more than $p^2 + p - 1$ sets of conjugate operators, so that the fact that a group of order p^m has $p^2 + p - 1$ sets of conjugate operators is a characteristic property of the non-abelian groups of order p^3. This fact results almost directly from the fact that the number of the sets of conjugate operators of a group is always larger than the number of the sets of conjugate operators in its quotient group with respect to any one of its non-identity invariant subgroups.

From what precedes it results that the smallest number of sets of conjugate operators in a prime power non-abelian group is five and that the two non-abelian groups of order 8 are the only prime power groups which separately contain exactly five sets of conjugate operators. It therefore results that if a group contains exactly three sets of conjugate operators and is non-abelian its order is divisible by at least two distinct prime numbers and when its order is divisible by exactly two distinct prime numbers it must be solvable. It must therefore contain an invariant subgroup of prime index and this index could clearly not exceed 2. The order of this invariant subgroup must be 3. That is, *the group of order 3 and the non-cyclic group of order 6 are the only two groups which satisfy the condition that all their operators appear in three and only three sets of conjugates under the group.*

To simplify some of the consideration which follow it may be desirable to formulate here the theorem that if a group G contains an invariant subgroup of prime index p which involves c sets of conjugate operators then the number of the sets of conjugate operators in G cannot be less than $p + (c - 1)/p$. This theorem results directly from the fact that in the quotient group there are at least $p - 1$ sets of conjugates and the number of the sets of conjugates in G resulting from the operators in the given invariant subgroup cannot be less than $(c - 1)/p + 1$. In the case of the theorem at the close of the preceding paragraph $p = 2$ and $c = 3$.

The only abelian groups which separately contain exactly four sets of conjugate operators are the two groups of order 4. It follows from the theorem noted above that if a group G is of prime power order it cannot

contain exactly four sets of conjugate operators. If its order is divisible by two and only two distinct prime numbers it involves an invariant subgroup of prime index since it is solvable. This index is either two or three. If it is two, the order of the given invariant subgroup is odd, for if it were even two of the four sets of conjugates operators in G would be composed of operators of order 2 and hence all the operators of odd order in G would be conjugate under G.

This invariant subgroup of index two could not be of order 6 since the symmetric group of this order is a complete group. It therefore results that the given invariant subgroup of index two under G is the group of order 5 and G is the dihedral group of order 10. When the given invariant subgroup is of odd prime index under G it must be of index three and G is the tetrahedral group. That is, *if a group involves exactly four sets of conjugate operators it is one of the two groups of order 4 when it is abelian and when it is non-abelian it is either the dihedral group of order 10 or the tetrahedral group.* The latter group is simply isomorphic with the alternating group of degree four.

If a group contains exactly five sets of conjugate operators and is abelian it is the group of order 5. It was noted above that when a non-abelian prime power group contains exactly five sets of conjugate operators it is one of the two non-abelian groups of order 8. It should be emphasized that when the order of a group is divisible by a prime number p the number of its sets of conjugate operators cannot be less than the number of different orders of the divisors of p and $p - 1$ for the different such prime numbers. This theorem results directly from the fact that the group of isomorphisms of the group of order p is cyclic. Hence it results that if a group contains exactly five sets of conjugate operators its order cannot be divisible by a larger prime number than seven.

If the order of such a group is divisible by seven and contains only one subgroup of order 7 it is the dihedral group of order 14 or the semi-metacyclic group of order 21. In both of these cases the order of G is divisible by two and only two distinct prime numbers. In general, if its order is divisible by two and only two distinct prime numbers it must be solvable and hence it must contain an invariant subgroup of prime index. This index can obviously not exceed three and when it is three the corresponding invariant subgroup cannot be non-abelian since its central quotient group would then be non-cyclic and of order 4. It could not be the non-twelve group of order 24 since this group contains seven sets of conjugate operators.

The preceding considerations were greatly simplified by the fact that we were generally dealing with solvable groups. When the number of the sets of conjugate operators is five we can no longer assume that G is always solvable since the simple group of smallest composite order contains exactly

five sets of conjugate operators. This group is of order 60 and is known to be simply isomorphic with the alternating group of degree five. One of the earliest workers in group theory, E. Galois (1811–1832), noted already that this group is simple and many of its other properties have received much attention since then.

SOME THEOREMS IN FINITE FIELD THEORY WITH APPLICATIONS TO FERMAT'S LAST THEOREM

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The first result we shall consider is as follows:

Theorem I. *If the relation*

$$a_{m-1}x^{m-1} + a_{m-2}x^{m-2} + \ldots + a_0 = 0, \tag{1}$$

with coefficients in a finite field, F, has exactly k solutions x in F, and such that $x^m = 1$, then the cyclic matrix

$$\begin{vmatrix} a_0 & a_1 \ldots a_{m-1} \\ a_{m-1} & a_0 \ldots a_{m-2} \\ \ldots\ldots\ldots\ldots\ldots\ldots \\ \ldots\ldots\ldots\ldots\ldots\ldots \\ a_1 & a_2 \ldots a_0 \end{vmatrix} \tag{2}$$

is of rank $m - k$.

For a finite field of order p, a prime, and for $m = p - 1$, this result is due to König.[1] As our result may be proved by following closely the steps in the argument employed by Kronecker[1] (replacing $(p - 1)$ by $(p^n - 1)$ and $x^{p-1} = 1$ by $x^m = 1$), for proving König's theorem, the details of the proof will not be given here.

Dickson,[2] by extending a theorem due to Hurwitz,[3] obtained the following:

Let $f(x)$ be a polynomial, and let F be a finite field of order p^n which includes the coefficients. Then the number N of distinct roots $\neq 0$ of $f(x) = 0$, which belong to the field of order p^n, satisfies the relation

$$N + 1 \equiv C_0 + C_s + C_{2s} + \ldots \pmod{p},$$

where $s = p^n - 1$ *and*

$$f(x)^{p^n-1} \equiv C_0 + C_1x + C_2x^2 + \ldots$$

For $n = 1$, this becomes the Hurwitz[3] theorem.

We shall find it convenient to set up some results which are obtained by modification of the ideas of Hurwitz and Dickson. In the result just mentioned, Dickson generalizes Hurwitz's original notions by asking the number of solutions in any finite field which includes the coefficients of the original equation. We may go in the other direction and ask what solution our equation has within certain subsets of elements in the finite field $F(p^n)$ which includes the coefficients. For example, consider the polynomial, $f(x)$, with coefficients included in a $F(p^n)$, and suppose that ρ is a primitive root of $x^a = 1$ in $F(p^n)$; $p^n - 1 \equiv 0 \pmod{a}$. Let our equation be

$$f(x) = 0, \tag{3}$$

and consider

$$\sum_{t=0}^{a-1} (1 - f(\rho^t)^{p^n-1}). \tag{4}$$

This obviously equals, in the finite field, the number N of distinct solutions of equation (3) which lie in the set

$$1, \rho, \rho^2, \ldots \rho^{a-1}.$$

To simplify equation (4), write

$$(f(x))^{p^n-1} = C_0 + C_1x + \ldots. \tag{5}$$

We note that

$$\left.\begin{aligned} \sum_{h=0}^{a-1} \rho^{sh} &= 0; \qquad s \not\equiv 0 \pmod{a}, \\ \sum_{h=0}^{a-1} \rho^{sh} &= a; \qquad s \equiv 0 \pmod{a}. \end{aligned}\right\} \tag{6}$$

so that equation (4), using equation (5), gives

$$N = a - a(C_0 + C_a + C_{2a} + \ldots), \tag{7}$$

in the field.

The above method may be further extended. Let

$$f(x_1, x_2, \ldots, x_n) = 0 \tag{8}$$

where $F(p)^n$ is any finite field including the coefficients. Further, let ρ_i be a primitive root in the $F(p^n)$ of $= x_i^{a_i} = 1$;

$$p^n - 1 \equiv 0 (\text{mod } a_i),$$

$$i = 1, 2, \ldots, n.$$

We now seek all the distinct sets of solutions of (8) for $x_1, x_2, \ldots, x_n$, which are in the field $F(p^n)$ and which are also included among the ρ_i^k's. If N_n is this number, then we have

$$N_n = \sum (1 - (f(x_1, x_2, \ldots, x_n))^{p^n - 1}) \tag{9}$$

where the summation extends over all the expressions obtained by letting x_i range independently over each of the elements

$$1, \rho_i, \rho_i^2, \ldots, \rho_i^{a-1};$$

$$i = 1, 2, \ldots, n.$$

Set

$$f(x_1, x_2, \ldots, x_n) = \sum C(e_1, e_2, \ldots, e_n) x_1^{e_1} x_2^{e_2} \ldots x_n^{e_n}$$

where the coefficients C are in $F(p^n)$. When x_i ranges over the ρ_i's; $i = 1, 2, \ldots, n$, we obtain, using equation (6)

$$\sum_{\rho} f(x_1, x_2, \ldots, x_n) = a_1 a_2 \ldots a_n \sum C(e_1' a_1, \quad e_2' a_2, \ldots, e_n' a_n)$$

where the summation on the right extends over all multiples $e_1' a_1$ of a_1 which are included among the e_1's, all multiples $e_2' a_2$ of a_2 included among the e_2's, and so on, for all the values of e_i; $i = 1, 2, \ldots, n$. Hence equation (9) becomes

$$N_n = A - A \sum C(e_1' a_1, e_2' a_2, \ldots, e_n' a_n) \tag{10}$$

where

$$A = \prod_{i=1}^{n} a_n.$$

We then have

THEOREM II. *If*

$$f(x_1, x_2, \ldots, x_n) = 0$$

is a polynomial, p^n is the order of any finite field $F(p^n)$ including the coefficients of f, and N_n is the number of sets of solutions $(x_1, x_2, \ldots, x_n)$ such that each $x_i, i = 1, 2, \ldots n$, satisfies in the $F(p^n)$, the equation $x^{a_i} = 1$, where $p^n - 1 \equiv 0 (\text{mod } a_i)$, then, in the field, N_n is given by equation (10).

We now obtain various applications of Theorems I and II to the theory of finite fields and to Fermat's last theorem. In another paper[4] the writer obtained the criteria

$$\binom{c}{s} + \binom{c}{s+l} + t^l + \binom{c}{s+2l} t^{2l} + \ldots \equiv 0 (\text{mod } p) \quad (11)$$

for the solution of

$$x^l + y^l + z^l = 0 \quad (12)$$

where l is an odd prime, $y \equiv 0 (\text{mod } l)$; $(xz, l) = 1$, p is a prime, $(p, l) = 1$, $(xyz, p) = 1$, and where, if $\mathfrak{p}$ is a prime ideal divisor of p in the field $k(\zeta)$, $\zeta = e^{2i\pi/l}$, then

$$c = \frac{N(\mathfrak{p}) - 1}{l}$$

and $\mathfrak{p}$ belongs to an exponent which is prime to l; $s = 1, 2, \ldots, l-1$; $y/x = t$. Here also, as usual,

$$\binom{a}{b} = 0$$

if $b > a$.

Applying Theorem I of the present paper to the relation (2) of our former paper[4] we find that the matrices (11) and (11a) of the latter are of rank $\leqq c - 2$. Also if $(xyz, l) = 1$ then (11) and (11a) are of rank $\leqq c - 6$ for p sufficiently large

The criteria of Kummer for the solution of equation (12) in case I are as follows: *If $(-t)$ is any of the quantities x/y, y/x, z/x, x/z, y/z, z/y, then*

$$\left.\begin{aligned} B_n f_{p-2n-1}(t) &\equiv 0 (\text{mod } l); \\ f_{p-2}(t) &\equiv 0 (\text{mod } l); \\ n &= 1, 2, \ldots, \frac{l-3}{2}; \end{aligned}\right\} \quad (13)$$

where $B_1 = 1/2$, $B_2 = 1/30$, etc., are the Bernoulli numbers and

$$f_a(t) = t + 2^a t^2 + \ldots + (l-1)^a t^{l-1}.$$

If $s = p - 2n - 1$, then we examine the relation

$$f_s(t) \equiv 0 (\text{mod } p). \quad (14)$$

The above values for t show that this relation holds also for $1/t$, $(1-t)/t$, $t/(1-t)$, $1-t$, $1/(1-t)$ after using $x + y + z \equiv 0 (\text{mod } l)$. (Note that t is here used in a different sense than in equation (11).) These six quantities are incongruent modulo l unless $t \equiv -1, +2$ or $-1/2$ or $t^2 - t + 1 \equiv 0$. The last combination is known to be inconsistent with equation (13) and the first holds only if $2^{l-1} \equiv 1 (\text{mod } l^4)$. If equation (14) holds for six incongruent values then the cyclic matrix

$$\begin{vmatrix} 1^s & 2^s \ldots (l-1)^s \\ (l-1)^s 1^s \ldots (l-2)^s \\ \ldots\ldots\ldots\ldots\ldots \\ \ldots\ldots\ldots\ldots\ldots \\ 2^s & 3^s \ldots \quad 1^s \end{vmatrix}$$

is of rank $\leqq l - 9$, since relation (14) is satisfied by $t \equiv \pm 1$ and $t \equiv 0$, and none of these lead to six incongruent values of t, modulo l, in fact $t \equiv 1$ is impossible from equation (12), and also $t \not\equiv 0$ by hypothesis.

We now apply Theorem II to the equation

$$au^m + bv^m + 1 = 0 \tag{15}$$

where $abuv \neq 0$, $mc = p^n - 1$, p prime, and seek the number N of its distinct solutions (u^m, v^m) in a finite field $F(p^n)$ including a and b. Here two solutions (u^m, v^m) and (u_1^m, v_1^m) are regarded as the same if and only if $u^m = u_1^m$ and $v^m = v_1^m$. Then Theorem II gives

$$N = \sum_{\rho_1, \rho_2} (1 - (a\rho_1 + b\rho_2 + 1)^{p^n - 1}) \tag{16}$$

where ρ_1 and ρ_2 each range independently over the distinct roots of $z^c = 1$ in $F(p^n)$. Now, if $i = p^n - 1 - h$, then

$$(a\rho_1 + b\rho_2 + 1)^{p^n - 1} = \sum_{h=0}^{p^n - 1} (a\rho_1 + 1)^h (\rho_2 b)^i (-1)^h$$

since

$$\binom{p^n - 1}{h} \equiv (-1)^h \pmod{p}.$$

Also

$$(a\rho_1 + 1)^h = \sum_{s=0}^{h} \binom{h}{s} (a\rho_1)^s.$$

Applying the last two relations to equation (16) gives

$$N = c^2 - c^2 \sum_{k=0}^{m} \sum_{r=0}^{k} \binom{kc}{rc} a^{rc} b^{mc - kc}$$

in the field. This reduces to a bit simpler form by noting that the term on the right corresponding to $k = 0$ is c^2, so that

$$N = -c^2 \sum_{k=1}^{m} \sum_{r=0}^{k} \binom{kc}{rc} a^{rc} b^{mc - kc}. \tag{17}$$

If $n = 1$, that is, the quantities a and b correspond to residue classes modulo p, then we may write

$$N \equiv -c^2 \sum_{k=1}^{m} \sum_{r=0}^{k} \binom{kc}{rc} a^{rc} b^{mc-kc} (\text{mod } p).$$

Let now $a = b = 1$, and $n = 1$, then equation (17) gives the result that N in equation (18) is now the number of solutions (u, v) of

$$u^m + v^m + 1 \equiv 0 (\text{mod } p) \tag{19}$$

where $(uv, p) = 1$; $p = 1 + cm$, which is related to Fermat's last theorem.

Return now to the consideration of equation (15). If we write $[h, k]$ for the number of distinct sets (s, t) such that

$$r^{sm+h} = r^{tm+k} + 1$$

in $F(p^n)$, r being a primitive root of F, it is known that[5] and

$$\sum_{i=0}^{m-1} [i, 0] = c - 1$$

$$\sum_{i} [i, j] = c$$

$i = 0, 1, 2, \ldots, m - 1$; $j = 1, 2, \ldots, m - 1$. Hence $[i, j] \leqq c$. For $n = 1$, then $c < p$, and we have

THEOREM III. *The number of sets of distinct integral solutions (u^m, v^m) of*

$$au^m + bv^m + 1 \equiv 0 (\text{mod } p)$$

where a and b are integers, p is prime; $(abuv, p) = 1$; m odd; $p - 1 = mc$; is the least residue, $\geqq 0$, of

$$-c^2 \sum_{k=1}^{m} \sum_{r=0}^{k} \binom{kc}{rc} a^{rc} b^{mc-kc}$$

modulo p.

[1] Raussnitz, *Math. and Naturw. Berichte aus Ungarn*, **1**, 266–275 (1882–1883); Rados, *Jour. für Math.*, **99**, 258–260 (1886); Kronecker, *Vorlesungen über Zahlentheorie*, **1**, 389–415 (1901), including additions by Hensel (Kronecker refers to Königs' theorem in several places there as "sehr elegante" and "wichtige"). For other generalizations, see numerous references in Dickson's *History of Theory of Numbers*, vol. 1, pp. 226–233.

[2] *Bull. Amer. Math. Soc.*, **14**, 313 (1907–1908).

[3] *Archiv. Math. Phys.*, **5** (3), 17–27 (1903).

[4] *Proc. Nat. Acad. Sci.*, **28**, 144 (1942).

[5] Mitchell, *Ann. Math.*, **17**, 165 (1916). The trinomial equation (15) has been extensively studied. See references cited here by Mitchell, as well as Mitchell, *Ann. Math.*, **18**, 120 (1917). Dickson, *Am. Jour. Math.*, **57**, 391, 463 (1935); *Trans. Amer. Math. Soc.*, **37**, 363 (1935).

ON TRINOMIAL CONGRUENCES AND FERMAT'S LAST THEOREM

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In another paper[1] we obtained two theorems (numbered I and II) concerning finite fields, obtaining therefrom explicit expressions for the number of sets of solutions of certain equations which were applied, in special cases, to Fermat's last theorem. The present article deals with other results along these lines which involve trinomial congruences.

Applying Theorem III of F to Theorem IV of another paper[2] of the author's we obtain:

THEOREM I. *If it is possible to find a prime p such that $p = 1 + cl$; l an odd prime such that*

$$-c^2 \sum_{k=1}^{l} \sum_{r=0}^{k} \binom{kc}{rc} \tag{1}$$

is divisible by p and $c \not\equiv 0 (\mathrm{mod}\ l)$ then

$$x^l + y^l + z^l = 0 \tag{2}$$

has no solution if $(xyz, l) = 1$.

Consider

$$au^m + bv^m + 1 \equiv 0 (\mathrm{mod}\ p) \tag{3}$$

where all the symbols represent integers $(abuv, p) = 1$; p prime. This gives

$$(au^m + 1)^c \equiv (-1)^c b^c v^{mc} (\mathrm{mod}\ p),$$

$$\equiv (-1)^c b^c (\mathrm{mod}\ p),$$

using Fermat's Theorem and $mc = p - 1$. Expansion of the left-hand member gives, again using the theorem just mentioned,

$$\binom{c}{c-1} a^{c-1} u^{m(c-1)} + \binom{c}{c-2} a^{c-2} u^{m(c-2)} + \ldots + \binom{c}{1} au^m + s \equiv 0 (\mathrm{mod}\ p)$$

where

$$s = a^c + 1 + (-1)^{c+1} b^c.$$

We now apply Theorem I of the first paper to eliminate u^m and we find

$$\begin{vmatrix} a\ C_1\ a^2C_2 \ldots a^{c-1}C_{c-1}\ sC_0 \\ a^2C_2\ a^3C_3 \ldots\ldots sC_0\ aC_1 \\ \ldots\ldots\ldots\ldots\ldots\ldots \\ \ldots\ldots\ldots\ldots\ldots\ldots \\ sC_0\ aC_1 \ldots a^{c-2}C_{c-2}\ a^{c-1}C_{c-1} \end{vmatrix} \equiv 0,$$

modulo p, where

$$C_i = \binom{c}{i};$$

but this criterion looks much more complicated than the condition in Theorem III of *F*.

We shall now present still another method for attacking equation (3), which is due to the late H. H. Mitchell.

If $\theta = e^{2i\pi/p-1}$ then in the field $k(\theta)$ an ideal prime factor of (p) is $(\theta - v, p) = \mathfrak{p}$, where v is a primitive root of p in the rational field. Then

$$u^m \equiv v^{rm} \equiv \omega^r (\text{mod } \mathfrak{p})$$
$$v^m \equiv v^{sm} \equiv \omega^s (\text{mod } \mathfrak{p})$$

where $\omega = e^{2i\pi/c}$, and for some r and s. Hence equation (3) becomes

$$a\omega^r + b\omega^s + 1 \equiv 0 (\text{mod } \mathfrak{p}).$$

Now take the norm of the left-hand member of this in $k(\omega)$; since said norm is rational it follows that

$$N(a\omega^r + b\omega^s + 1) \equiv 0 (\text{mod } p). \qquad (4)$$

The left-hand member is now independent of p and l. It is clear then that unless we have an r and s such that this quantity reduces to zero then equation (3) is impossible for sufficiently large values of p. For the case $a = b = 1$, it is known that there is an r and s such that

$$\omega^r + \omega^s + 1$$

vanishes, if and only if $c \equiv 0 \pmod 3$. Also

$$\begin{aligned} |\omega^r + \omega^s + 1| &\leqq |\omega^r| + |\omega^s| + 1 \\ &\leqq 1 + 1 + 1 \\ &\leqq 3 \end{aligned}$$

or

$$|N(\omega^r + \omega^s + 1)| \leqq 3^{\varphi(c)},$$

$\varphi(c)$ being the indicator of c, whence the result, due to Mitchell,[3]

THEOREM II. *If c is a given integer $\not\equiv 0 (\text{mod } 3)$, and there is a prime p such that $p = 1 + mc$ and*

$$p > 3^{\varphi(c)}$$

then

$$u^m + v^m + 1 \equiv 0 (\text{mod } p)$$

has no integral solutions (u, v); $(uv, p) = 1$.

It is known that (Dickson[4]) equation (3) is always satisfied in integers if $p = 1 + mc$, m is prime and

$$p \geqq (m - 1)^2(m - 2)^2 + 6m - 2$$

The question as to the congruence (5) having solutions or not for a prime p of the form $1 + mc$, which does not satisfy the last inequality or that given in Theorem II, is, in general, one of the great mysteries of number theory.

Employing Theorem II of this paper together with Theorem IV of another paper[2] we find

THEOREM III. *If c is a given even integer $\not\equiv 0$ (mod 3) and it is possible to find two primes l and p such that $p = 1 + cl$; $l > c$; and $p > 3^{\varphi(c)}$; then*

$$x^l + y^l + z^l = 0$$

is impossible in integers, with $(xyz, l) = 1$. Here $\varphi(c)$ is the indicator of c.

[1] These PROCEEDINGS, **30**, 362–367 (1944). This paper will be referred to as *F*.

[2] *Ann. Math.*, **27**, 56 (1926).

[3] This theorem and proof were communicated to me verbally by Prof. Mitchell. This happened some time in the year 1926, if I recall correctly. So far as I know he never published this material.

[4] *Jour. für die Reine u. Angew. Math.*, **135**, 134–141, 181–88 (1909).

ON THE INTEGRAL EQUATIONS OF CONTINUOUS DYNAMICAL SYSTEMS

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NEW YORK, N. Y.

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1. Introduction.—The dynamical systems are the one-dimensional ones considered recently[1] and are governed by the vector equation

$$\Upsilon(x, t) := \int_a^b \mathcal{G}(x, \xi)\alpha(\xi) \frac{\partial \Upsilon(\xi, t)}{\partial t} d\xi \qquad (1)$$

in which the components of Υ: are the coördinates, velocities and internal

forces of the system and where $\mathcal{G}$ is the matrix of the Green's functions and $\mathfrak{A}$ the matrix of the conservative parameters (inertial and elastic coefficients).

If the variables are separable, as it is necessary to suppose, there exist relations of the form $\Upsilon_i(x, t) = W_i(x)T_i(t)$, $i = 1, 2, \ldots, n$ for the components of the vector in equation (1) and if we define B_{ij} by the equation

$$\int_a^b K_{ij}(x, \xi)W_j(\xi)d\xi = B_{ij}W_i(x)$$

in which K_{ij} is the element of $\mathcal{G}\mathfrak{A} = \mathcal{K}(x, \xi)$ in the ith row and jth column, then the time factors are components of the vector T: which satisfies the equation $\mathfrak{B}\dot{T}: = T:$ in which $\mathfrak{B} = (B_{ij})$. This equation in T: has the solution $T: = \epsilon^{\mu t}C:$ provided $C:$ and μ satisfy the equation $\mu\mathfrak{B}C: = C:$. When a solution for $C:$ of this equation exists, the substitution $C_iW_i(x) = \epsilon^{-i\beta_i}U_i(x)$ into equation (1) gives the integral equation

$$\mathcal{E}U(x): = \mu\int_a^b \mathcal{G}(x, \xi)\mathfrak{A}(\xi)\mathcal{E}U(\xi):d\xi$$

in which $\mathcal{E}$ is the constant diagonal matrix[2] $[\epsilon^{-i\beta_i})$, for the determination of the β's, $U(x)$: and μ. On the hypothesis that the μ's are distinct, a necessary and sufficient condition that the variables be separable is that the B's be constants.

This integral equation and its *associate*, written in the form

$$\Phi(x): = \mu\int_a^b \mathcal{K}(x, \xi)\Phi(\xi): d\xi, \qquad \cdot\Psi(x) = \mu\int_a^b \cdot\Psi(\xi)\mathcal{K}(\xi, x)d\xi \qquad (2)$$

where $\mathcal{K}$ is in general a non-symmetric matric kernel, are to be found, in effect, in Fredholm's classic paper[3] but, as is well known, development of the theory has remained seriously incomplete, when the kernel is not restricted to be symmetric, and notably in directions admitting any aphoristic geometrical restatement of the results. In this regard the theory of equation (2) is in remarkable contrast to the theory of the *conjugated* pair of equations

$$\phi(x) = \kappa\int_a^b K(x, \xi)\psi(\xi)d\xi, \qquad \psi(x) = \kappa\int_a^b \phi(\xi)K(\xi, x)d\xi$$

of Erhard Schmidt[4] which has a complete analogy in the abstract theory of Hilbert space but, nevertheless, slight and insignificant contact with the differential equations of dissipative elastokinetics.

Directly connected with the differential equations of such dynamical systems and their adjoint equations, on the other hand, is the *adjoint* pair of integral equations

$$Y(x): = \mu\int_a^b \mathcal{G}(x, \xi)\mathfrak{A}(\xi)Y(\xi): d\xi, \qquad \cdot Z(x) = \mu\int_a^b \cdot Z(\xi)\mathfrak{A}(\xi)\mathcal{G}(\xi, x)d\xi$$

studied by Birkhoff & Langer[5] who obtained formal results of a kind indicated by the theory of the affine transformation of an n-dimensional

space into itself and among them the bilinear expansion $\mathcal{G}(x, y) = \Re\Sigma\lambda_r Y_{(r)}(x) \cdot Z_{(r)}(y)$, $\lambda_r = \mu_r^{-1}$ for the Green's matrix and equivalent to the expression $\mathcal{K}(x, y) = \Re\Sigma\lambda_r\Phi_{(r)}(x) \cdot \Psi_{(r)}(y)$ for the kernel $\mathcal{K}$.

There is evidence that there exists an important class of kernels the members of which either have this expansion or their iterates have a similar one. In fact, the representation for the iterated kernel

$$\mathcal{K}^s(x, y) = \Re\Sigma \frac{\Phi_{(r)}(x) \cdot \Psi_{(r)}(y)}{\mu_r^s} \qquad (3)$$

is known to be valid in the cases of the vibrating string and of the electrical transmission line, in the usual cases where the Green's function satisfies the equation $d^2G(x, y)/dx^2 = 0$, and for the non-symmetric kernel in the integral equation for the thermo-mechanical motions of an elastic rod[6] with $s = 1$. It is known that the series converges absolutely and uniformly in both variables to the kernel or iterated kernel with $s = 1$ if the kernel is symmetric, continuous and positive definite (Mercer), with $s = 2$ if the kernel is symmetric and continuous (Erhard Schmidt). The series is also known (Garbe,[7] Mercer[8]) to converge to a non-symmetric kernel of the form $K(x, y) = \alpha(x)k(x, y)$ for $k(x, y)$ "allgemein" or for $K(x, y)$ "completely symmetrisable" under certain conditions. The modal numbers of a real, symmetric and segmentally continuous kernel are either finite in number or enumerably infinite and converge to ∞[9] and the same is true for the non-symmetric and only segmentally continuous matric kernel of the electrical transmission line. In fact, the literature of integral equations and of elastokinetics would appear to contain very few if any examples where the modal numbers have or could have any finite cluster point.

In view of this evidence it is obvious that the class of kernels for which equation (3) is in some sense valid and for which the modal numbers have no finite cluster point is sufficiently extensive and important to warrant such steps forward as are possible on the basis of these properties even although the elusive problem of characterization of the class remains unsolved. The step essayed in the following paragraphs is in the direction of a more explicit determination of the modal vectors and numbers.

Notation.—The notation used in this paper is a modification of that of Birkhoff & Langer. A line or row vector $(v_1, v_2, \ldots, v_n)$ is written $\cdot v$ but a column vector of elements u_i, $i = 1, 2, \ldots, n$ is written $u\cdot$. The inner product $\Sigma v_i u_i$ of a row vector $\cdot v$ and a column vector $u\cdot$ is written $\cdot vu\cdot$ and the outer product $(u_i v_j)$ is an $n \times n$ matrix with the element $u_i v_j$ in the ith row and jth column and is written $u\cdot\cdot v$. Script letters denote $n \times n$ matrices. As powers of the kernel matrix $\mathcal{K}$ do not occur in the work, the s-fold iterated integral

$$\int_a^b \int_a^b \ldots \int_a^b \mathcal{K}(x, \xi_1)\mathcal{K}(\xi_1, \xi_2)\ldots\mathcal{K}(\xi_s, y)d\xi_1\, d\xi_2 \ldots d\xi_s$$

is written simply $\mathcal{K}^{s+1}(x, y)$.

2. Determination of the Modal Vectors and Numbers.—The method for the computation of the first modal number and function of any real symmetric kernel first given by Erhard Schmidt and the extension of the method by Koch to the cases of the second, third, ... modal number and function in succession have been still further generalized by Ingram[1] to the case of a vector integral equation with non-symmetric matric kernel. Noteworthy steps in this generalization are the recognition of the existence of possible differences in phase among the various components of any modal vector $\Upsilon(x, t)$:, the simultaneous computation of the Φ's and Ψ's, the matric concepts involved and the algebraic problem which is the end-product of the method. Certain sufficient conditions for the convergence of the generalized procedure are now considered.

The relations of orthogonality

$$\left.\begin{aligned} \int_a^b \cdot\Psi_{(i)}(x)\Phi_{(j)}(x) : dx = 0 = \int_a^b \cdot\Psi_{(i)}(x)\bar{\Phi}_{(j)}(x) : dx \qquad i \neq j \\ \int_a^b \cdot\Psi_{(i)}(x)\bar{\Phi}_{(i)}(x) : dx = 0 \qquad \mu_i \neq \bar{\mu}_i \\ \int_a^b \cdot\Psi_{(i)}(x)\Phi_{(i)}(x) : dx = 2 \end{aligned}\right\} \quad (4)$$

between the modal functions are first derived from equation (2) in the usual way: the last equation is a matter of agreement.

LEMMA: *If the series* $\Re\Sigma\lambda_r^s\Phi_{(r)}(x) :\cdot\Psi_{(r)}(y)$ *is segmentwise uniformly and boundedly convergent (with respect to* y*) to* $\mathcal{K}^s(x, y)$ *for every fixed value of* x *on* $a \leqslant x \leqslant b$ *and for some natural number* s*, if* $\Xi(x)$: *is any integrable vector orthogonal to* $\cdot\Psi_{(1)}(x)$, $\cdot\Psi_{(2)}(x)$, ..., $\cdot\Psi_{(\kappa-1)}(x)$ *but not to* $\cdot\Psi_{(\kappa)}(x)$ *and such that* $\Sigma\int_a^b \cdot\Psi_{(r)}(y)\Xi(y) : dy$ *converges absolutely, and if the modal numbers can be enumerated in order of increasing modulus and have no finite accumulation point, then the vectors*

$$\mathfrak{P}^s(x) : = \int_a^b \mathcal{K}^s(x, y)\Xi(y) : dy, \qquad \mathfrak{P}^{s+1}(x) : = \int_a^b \mathcal{K}(x, y)\mathfrak{P}^s(y) : dy$$

are either constant multiples of one and the same function of x *or become so as* $s \to \infty$.

Proof. The first step is to make it clear that both sides of equation (3) may be multiplied by $\Xi(y)$: and integrated term-by-term with respect to y so as to give

$$\mathfrak{P}^s(x) : = \int_a^b \mathcal{K}^s(x, y)\Xi(y) : dy = \Re\Sigma\lambda_r^s\tau_r\Phi_{(r)}(x) :, \ \tau_r = \int_a^b \cdot\Psi_r(y)\Xi(y) : dy$$

an equation in which the series converges. This result follows from the definition of a uniformly and boundedly convergent series and from the fact that a segmentwise uniformly and boundedly convergent series of terms which are functions of y may be multiplied term-by-term by any integrable function and integrated term-by-term to give the integral of the product of the sum limit multiplied by the function.

It is to be noted next that the modal functions are bounded since the kernel is bounded from the definition of the Green's matrix and because $\mathfrak{A}(x)$ is naturally bounded (but possibly discontinuous at any number of points) and accordingly any modal function which is finite for one value of x is finite for all values on $a \leqslant x \leqslant b$. If M: is a vector of positive elements such that $|\Phi_{(r)i}(x)| \leqslant M_i$, all i, then the last equation becomes the inequality

$$|\mathfrak{P}^s(x)|: \leqslant M:\{|\lambda_\kappa^s \tau_\kappa| + |\lambda_{\kappa+1}^s \tau_{\kappa+1}| + \ldots\}.$$

But by hypothesis $\tau_\kappa + \tau_{\kappa+1} + \ldots$ converges absolutely and the moduli of the λ's form a decreasing sequence and tend to zero as a limit for $s = 1$ and tend to zero faster for $s > 1$. For sufficiently large s, therefore, the first non-zero term can be taken as an approximation to the series with an error for any value of x as small as desired short of zero. It follows that $\mathfrak{P}^s(x)$: and $\mathfrak{P}^{s+1}(x)$: are both approximately proportional to the same real vector $\mathfrak{N}\lambda_\kappa^s \tau_\kappa \Phi_{(\kappa)}(x)$: which is seen to be a diagonal matrix times the real vector $U_{(\kappa)}(x)$:.

The lemma just proved justifies a procedure for a more explicit determination of the modal functions and numbers. If, in conformity with the equation $\mathfrak{B}\dot{T}: = T$: satisfied by the time factor in the variables of equation (1), the substitution $\mathfrak{T}_i(x, t) = \epsilon^{\alpha t} \cos(\omega t - \beta_i) U_i(x)$ is made, then equation (1) takes the form $\Phi(x): = \mu \int_a^b \mathfrak{K}(x, \xi)\Phi(\xi): d\xi$ with, as before $\mu = \alpha + \omega$, $\Phi(x): = \mathcal{E}U(x):$, $\mathcal{E} = [\epsilon^{-\iota\beta_i}]$. By the lemma, $\int_a^b \mathfrak{K}^s(x, \xi)\Xi(\xi): d\xi$ gives, at least approximately, the components $\Phi_{(r)1}(x), \Phi_{(r)2}(x), \ldots, \Phi_{(r)n}(x)$ each to within a constant factor. It follows directly, if, as a matter of notation $\Phi(x): = W(x): - \iota X(x):$, that there are the at least approximate equations

$$W_i(x) = \eta_i \mathfrak{P}_i^s(x), \qquad X_i(x) = \eta_i \tan \beta_i \mathfrak{P}_i^s(x) \tag{5}$$

where η_i is a constant factor and in which all quantities are real when, as is always possible, $\Xi(x)$: is taken real. Substitution of these expressions into equation (3) gives

$$\left.\begin{aligned} \eta_i \mathfrak{P}_i^s(x) &= \alpha \Sigma \eta_j \int_a^b K_{ij}(x, \xi)\mathfrak{P}_j^s(\xi) d\xi \\ &\quad + \omega \Sigma \eta_j \tan \beta_j \int_a^b K_{ij}(x, \xi)\mathfrak{P}_j^s(\xi) d\xi \\ \eta_i \tan \beta_i \mathfrak{P}_i^s(x) &= -\omega \Sigma \eta_j \int_a^b K_{ij}(x, \xi)\mathfrak{P}_j^s(\xi) d\xi \\ &\quad + \alpha \Sigma \eta_j \tan \beta_j \int_a^b K_{ij}(x, \xi)\mathfrak{P}_j^s(\xi) d\xi \end{aligned}\right\} \tag{6}$$

a system of $2n$ equations in the unknowns $\alpha, \omega, \eta_1, \eta_2, \ldots, \eta_n, \tan \beta_1, \tan \beta_2, \ldots, \tan \beta_n$. When $\mathfrak{P}_i^s(x)$ and $\int_a^b K_{ij}(x, \xi)\mathfrak{P}_j^s(\xi) d\xi$ are multiples of the same function of x, all i and j, i.e., when $\int_a^b K_{ij}(x, \xi)\mathfrak{P}_j^s(\xi) d\xi = p_{ij}\mathfrak{P}_i^s(x)$ with p_{ij} a constant, then there is the system of $2n$ equations

$$\left.\begin{aligned} \eta_i &= \alpha\Sigma p_{ij}\eta_j + \omega\Sigma p_{ij}\eta_j \tan\beta_j \\ \eta_i \tan\beta_i &= -\omega\Sigma p_{ij}\eta_j + \alpha\Sigma p_{ij}\eta_j \tan\beta_j \end{aligned}\right\} (7)$$

to be solved for α, ω, the $n-1$ ratios η_i/η_1 and $n-1$ of the β's and in which the p's are known and one β is arbitrary. The ultimate validity of equation (7) is ensured when $\mu_1\bar{\mu}_1 < \mu_2\bar{\mu}_2 < \ldots$ and the μ's have no finite accumulation point and the p's are constants for then any error in equation (5) tends to zero as $s \to \infty$.

The constancy of the p's is connected with our fundamental assumption that the variables in equation (1) can be separated. Obviously, if the B's of the Introduction are constants then any μ must be a constant and the corresponding T: cannot be a function of x. The constancy of the B's is also a necessary condition for any T: to be a function of t only. For let $\mathfrak{I} = [T_1: T_2: \ldots T_n:]$ be a matrix of the fundamental solutions of the equation $\mathfrak{G}\dot{T}: = T:$. By hypothesis, the solutions of the equation $\det(\mu\mathfrak{G} - \mathfrak{g}) = 0$ are distinct so that $\det \mathfrak{I} \neq 0$. Hence $\mathfrak{G} = \mathfrak{I}(\dot{\mathfrak{I}})^{-1}$ and no element of $\mathfrak{G}$ can be a function of x. As has been seen in the proof of the lemma, $\mathfrak{P}_i^s(x)$ is approximately proportional to $U_{(s)i}(x)$ so that the ultimate constancy of the p's follows. When the variables cannot be separated, there are no modal functions and numbers.

The system (7) obviously is a linear one in the unknowns $\eta_1, \eta_2, \ldots, \eta_n, \eta_1 \tan\beta_1, \eta_2 \tan\beta_2, \ldots, \eta_n \tan\beta_n$ and so the problem may be expressed as that of solving the vector system

$$\left.\begin{aligned} \alpha\mathfrak{P}\eta: + \omega\mathfrak{P}\zeta: &= \eta: \\ -\omega\mathfrak{P}\eta: + \alpha\mathfrak{P}\zeta: &= \zeta: \end{aligned}\right\} (8)$$

in which, as a matter of notation, $\zeta_i = \eta_i \tan\beta_i$ and $\mathfrak{P} = (p_{ij})$. Real values of α and ω therefore exist which will reduce the rank of the matrix

$$\mathfrak{M} = \begin{bmatrix} \alpha\mathfrak{P} - \mathfrak{g} & \omega\mathfrak{P} \\ -\omega\mathfrak{P} & \alpha\mathfrak{P} - \mathfrak{g} \end{bmatrix}$$

to $2n-2$. The explicit formulae for the unknowns which accomplish this reduction in the case $n = 2$ have been applied to the case of the electrical transmission line.[1] The discussion is summarized in the following theorem.

THEOREM 1. *The hypotheses are* (1) *the modal numbers for equation* (2) *occur only in conjugate complex pairs such that* $\mu_1\bar{\mu}_1 < \mu_2\bar{\mu}_2 < \ldots$ *and have no finite accumulation point,* (2) $\mathfrak{K}^s(x, y)$ *can be expressed, for some* s, *as a finite sum or as a stepwise uniformly and boundedly convergent series of the form* (3), (3) $\Xi(x)$: *is a linear combination of* $\Phi_{(s)}(x):, \Phi_{(s+1)}(x):, \ldots$ *or has an absolutely and uniformly convergent representation in terms of these functions. The conclusions are, with* $\Xi(x)$: *taken real, that there exist real values*

of α and ω which will reduce the rank of $\mathfrak{M}$ to $2n - 2$, that such values are at least approximately the real and imaginary parts, respectively, of the modal number μ_κ for the equation (2) *and that the corresponding solution of the equation* $(\cdot\eta, \cdot\xi)\mathfrak{M}_T = 0$ *with one element each of the vectors taken arbitrarily gives, in the equations*

$$W_{(r)}(x) := [\eta]\int_a^b \mathfrak{K}^s(x, y)\Xi(y) : dy, \qquad X_{(r)}(x) := [\xi]\int_a^b \mathfrak{K}^s(x, y)\Xi(y) : dy$$

the modal function $\Phi_{(r)}$:.

3. The Subsidiary Modal Determinant.—Suppose there is a solution $\Phi(x)$: of equation (2). Then $\mathfrak{N}\Phi(x)$: with $\mathfrak{N}$ a diagonal matrix of complex numerical elements is also a solution provided only that the columnar contraction N: of $\mathfrak{N}$ be a solution of the equation $\mu\mathfrak{B}N := N$: in which the elements of $\mathfrak{B}$ are defined by the equation $\int_a^b K_{ij}(x, \xi)\Phi_j(\xi)d\xi = B_{ij}\Phi_i(x)$ equivalent to the definition in the Introduction. In fact, every solution of the equation $\mu\mathfrak{B}N := N$: for μ and corresponding N: gives a solution of equation (2), the proof being by contradiction.

If, instead of $\Phi(x)$:, we take $\mathfrak{N}_1\Phi(x)$: such that $\mathfrak{N}_1$: is any one of the solutions of the subsidiary equation $\mu\mathfrak{B}N := N$: and such that μ' is the corresponding modal number and suppose $\mathfrak{N}\mathfrak{N}_1\Phi(x)$: to be a modal vector having the modal number μ'' not necessarily the same as either μ' or μ, then reasoning parallel to that just given shows that the vector (NN_1): which is the columnar contraction of $\mathfrak{N}\mathfrak{N}_1$ satisfies the equation $\mu\mathfrak{B}(NN_1) := (NN_1)$: and so the set of $\mathfrak{N}$'s have closure under multiplication.

THEOREM 2. *If $\Phi(x)$: is any modal vector, then $\mathfrak{N}\Phi(x)$: is also a modal vector as, more generally, is $\mathfrak{N}_1\mathfrak{N}_2 \ldots \mathfrak{N}_k\Phi(x)$: provided merely that the $\mathfrak{N}$'s are the diagonal forms of any of the solutions of the equation $\mu\mathfrak{B}N := N$:.*

The modal numbers for the $\mathfrak{N}$'s are among the roots of the equation

$$det(\mu\mathfrak{B} - \mathfrak{g}) = 0.$$

[1] *Phil. Mag.*, **30**, 16 (1940); *Bull. Amer. Math. Soc.*, **48**, 153 (1942).

[2] A diagonal matrix of elements $a_1, a_2, \ldots, a_n$ is designated $[a_i]$.

[3] Fredholm, Ivar, *Acta Math.*, **27**, 371 (1903)

[4] Schmidt, Erhard, *Math. Annalen*, **63**, 461 (1907); in the notation of Stone, *Linear Transformations in Hilbert Space*, 1932, Schmidt's equations are written $\phi = T\psi$, $\psi = T^*\phi$, and T^* is called, following Schmidt, the "adjoint" of T.

[5] Birkhoff & Langer, *Proc. Amer. Acad. Arts Sci.*, **58**, 51–128 (1923).

[6] Kneser, *Integralgleichungen*, 2nd ed., 1922, pp. 199–212.

[7] Garbe, *Math. Annalen*, **76**, 538–542 (1914–1915).

[8] Mercer, *Proc. Roy. Soc. Lond.*, **A97**, 412 (1920).

[9] E. Schmidt, *Math. Annalen*, **63**, 446 (1907).